AN ABSTRACT OF THE DISSERATION OF

Matthew R. Sloat for the degree of Doctor of Philosophy in Fisheries Science presented on March 18, 2013

Title: Born to Run? Integrating Individual Behavior, Physiology, and Life Histories in Partially Migratory Steelhead and Rainbow trout (*Oncorhynchus mykiss*)

Abstract approved:

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Steelhead and rainbow trout are common names for marine-migratory (anadromous) and freshwater-resident forms of *Oncorhynchus mykiss*, a partially migratory salmonid fish. Anadromous and resident forms are sympatric and can produce offspring with a life history different from their own (i.e., steelhead parents can produce rainbow trout offspring and vice versa). The expression of these alternative life histories is a plastic response to individual patterns of energy acquisition, assimilation, and allocation during juvenile life stages. Individual performance during early stream life is of particular interest because of potential carry-over effects on subsequent growth and developmental trajectories. In a series of experiments in laboratory streams, I determined the influence of individual variation in energy metabolism on behavior, growth, and life-

history expression in *O. mykiss*. Individual variation in energy metabolism was a strong predictor of feeding territory acquisition by juvenile fish during the transition from dependence on maternal provisioning of egg yolk reserves to independent feeding. Feeding territory acquisition was positively associated with standard metabolic rate (SMR) under conditions of an abundant and predictable food supply. When the density of intraspecific competitors was manipulated, the association between SMR and territory acquisition was strongest at intermediate stocking densities, moderate at the highest stocking densities, and weakest at the lowest stocking densities. However, reducing the spatial predictability of food resources within streams reversed the influence of SMR on competitive outcomes. These experiments determined that variation in ecological conditions during early life stages imposes different selection regimes on juvenile *O. mykiss* and results in physiological divergence among cohorts. Subsequent rearing experiments determined that behavioral dominance influences rates of anadromy and freshwater maturation, most likely through the association between SMR and territory acquisition. In addition to the effects of behavioral dominance, I observed a significant influence of sex, rearing temperature, and individual growth trajectories on the expression of anadromy and freshwater maturation. Partially migratory populations of *O. mykiss* maintain an exceptionally diverse portfolio of life-history strategies. Results from this work lend insight into a suite of behavioral and physiological processes influencing individual life histories.

Born to Run? Integrating Individual Behavior, Physiology, and Life Histories in Partially Migratory Steelhead and Rainbow trout (*Oncorhynchus mykiss*)

by

Matthew R. Sloat

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of

the requirements for

the degree of

Doctor of Philosophy

Presented March 18, 2013

Commencement June 2013

Doctor of Philosophy dissertation of Matthew R. Sloat presented on March 18, 2013.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Matthew R. Sloat, Author

ACKNOWLEDGEMENTS

I couldn't have completed this dissertation without the help of a large community of people and organizations. First, I want to thank Gordie Reeves for bringing me to OSU and providing me with an amazing amount of freedom to follow my curiosity. My committee members, Jason Dunham, Mike Blouin, David Noakes, Mark Hixon, and Lorenzo Cianelli, were also instrumental in helping me through this process. I want to especially thank Jason Dunham for his generosity in sharing both time and resources. I also received generous financial support from a variety of people and organizations while at OSU: M. A. Ali, Neil Armantrout, Washington County Flyfishers, Flyfisher's Club of Oregon, Oregon Council Federation of Fly Fishers, Sunriver Anglers Club, Oregon Chapter American Fisheries Society's Carl Bond Memorial Scholarship, and Thomas G. Scott. An awful lot of people helped obtain and rear fish and run the experiments included here. Thanks to Rich Madden, Jack Palmer, Don Ratliff, Rod French, Joseph Oneil, Ryan Couture, staff at ODFW's Alsea and Clackamas hatcheries, Jerry Bartholemew, Jill Pridgeon, Don Stevens, Ruth Milston-Clements, Carl Schreck, Rob Chitwood, Brian Neilson, Art Bass, Matt Stinson, Stephanie Saunders, Mike Reeves, Rosie Gonzalez, Amy Lindsley, and Haley Ohms. My wife India was instrumental to every aspect of this research and also kept me close to sane through some lean years. Finally, out of respect for the lives of all of the fish that unwittingly and unwillingly participated in my dissertation research, I have done my best to ensure that this work contributes to an increased understanding of the ecology and conservation of our wild steelhead. Long may you run. . .

CONTRIBUTION OF AUTHORS

Dr. Gordon H. Reeves was an advisor and editor on all manuscripts included in this work.

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Chapter 1- Introduction

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The migration of animals has received considerable attention due the inherent drama involved in the long-distance movement of sometimes spectacular numbers of individuals (Dingle 1996). Ecologists have increasingly recognized that migratory species are major drivers of ecosystem structure and function (e.g., Wilson and Halupka 1995; Winemiller and Jepsen 1998; Polis et al. 2004). In many fish species, individuals may exhibit a wide range of migratory behavior (Chapman et al. 2011). Ontogenetic niche shifts involve migrations of thousands of kilometers for some individuals, while others remain sedentary by comparison, completing their entire life cycle within a narrow home range. Such a diversity of migratory behavior is termed partial migration (Chapman et al. 2011), and is exhibited by many species of salmonid fish (Jonsson and Jonsson 1993; Dodson et al. 2013). Partially migratory salmonid populations consist of anadromous individuals that undergo marine migrations before reaching maturity, as well as freshwater residents that complete their entire life cycle in freshwater streams. Given the potential ecological importance of migration, an increased understanding of the causes of variation in migratory behavior is fundamental to our understanding of the structure and function of aquatic ecosystems (Flecker et al. 2010).

Steelhead and rainbow trout are common names for alternative life-history forms within *Oncorhynchus mykiss*, a partially migratory salmonid fish. North American populations of *O. mykiss* are distributed from southern California to south-central Alaska (Behnke 2002). Populations inhabit coastal streams in relatively close proximity to the ocean, as well as interior watersheds as far as 1500 km inland (Busby et al. 1996). The term “steelhead” refers to anadromous individuals, while “rainbow trout” are freshwater

residents. Anadromous and resident forms are sympatric and can produce offspring with a life history different from their own (i.e., steelhead parents can produce rainbow trout offspring and vice versa) (Seamons et al. 2004; Christie et al. 2011; but see Zimmerman and Reeves 2000). Steelhead rear in freshwater streams for between one and seven years before undergoing the behavioral, morphological, and physiological changes (collectively referred to as smolting) that are necessary for life in the marine environment. Steelhead then spend between one and four years foraging in the North Pacific Ocean before returning to freshwater to complete reproduction. Rainbow trout exhibit considerable variation in the age at maturity, reproducing after one to eight years of rearing (Schill et al. 2010). After accounting for this wide variation in the timing of major life-history transitions and in the age at maturation, as many as 32 different developmental trajectories may be present in a single population of *O. mykiss* (Thorpe 2007).

While a simple dichotomy of “anadromy” versus “freshwater residency” belies the diverse array of developmental pathways within each form, this division does correspond with major differences in selective pressures experienced by these alternative phenotypes. Steelhead must delay reproduction in order to migrate to the rich feeding grounds of the temperate seas, but benefit from a larger size at maturity. Mortality during the smolt migration and early ocean occupancy may exceed 95%, decreasing the mean survival to reproduction for anadromous individuals. Rainbow trout have a higher survival to reproduction, an increased probability of repeat spawning (iteroparity), but reproduce at sizes that may be two orders of magnitude smaller than their anadromous counterparts (Fleming et al. 2004). Thus, anadromous and resident life histories are

characterized by major tradeoffs in survival to first reproduction as well as the size and age at reproduction.

The balance of these tradeoffs is likely to vary between the sexes because of differences between males and females in the strength of size-mediated fitness components (Hendry et al. 2004). The benefit of obtaining a large size at maturity through anadromy may be greater for females than males. Female reproductive success is typically limited by the production of gametes, rather than access to mates, and fecundity is closely related to body size (Quinn et al. 2011; Schill et al. 2010). In contrast to females, reproductive success in males is typically limited by access to mates rather than gamete production (Gross 1991; Fleming and Reynolds 2004). Consequently, males have evolved multiple tactics to gain access to females, which are in part linked to body size. Larger individuals attempt to dominate access to females through aggressive competition, whereas smaller individuals rely more on sneaking tactics to surreptitiously fertilize eggs during spawning (Fleming 1996). The size difference of males using alternative mating tactics can be considerable in salmonids, as the body mass of sneaker males is often two orders of magnitude lower than “fighter” males (Fleming et al. 2004). Despite this discrepancy in size, however, sneaking males can have significant reproductive success, and may fertilize over 50% of the eggs in some salmonid populations (Morán et al. 1996; Martinez et al. 2000; Garcia-Vazquez et al. 2001). Consequently, males are less dependent on large body size for reproductive success than females. Females should, therefore, receive a much greater benefit from anadromy than males (Hendry et al. 2004),

and this is reflected in the consistently higher frequency of females among outmigrating smolts in steelhead populations (Ohms 2012).

In addition to differences between the sexes, there is considerable variation among individuals in their sensitivity to proximate factors influencing life-history expression. Factors such as food availability and stream temperature influence individual life histories through their effects on growth and energy storage during juvenile rearing (Jonsson and Jonsson 1993). Thus, the expression of anadromous and resident phenotypes can be thought of as the outcome of individual resource economics. Resource economics include the amount of food resources an individual can acquire, assimilate, and allocate to competing energy uses (Bernardo and Reagan-Wallin 2002). Obviously, all organisms need to eat to survive, but individuals exhibit large differences in the quantity of food they need to support basic maintenance costs (e.g., Enders and Scruton 2005; Tyler and Buldoc 2008), as well as the amount of energy that they can acquire during competition for limited food resources (e.g., Keeley 2001; Reid et al. 2011). Once food is acquired, individuals also demonstrate differences in the efficiency of digestion and the amount of energy that can be assimilated from a given intake of food (e.g. Millidine et al. 2009; Van Leeuwen et al. 2011). Ultimately, the allocation of assimilated energy to competing functions such as maintenance, growth, storage, and maturation, determines individual growth and development trajectories, and is the process through which life histories emerge (Bernardo and Reagan-Wallin 2002).

Standard metabolic rate (SMR), the measure of the rate at which an animal burns calories to sustain basic physiological processes, is a fundamental trait underlying

individual resource economics. In salmonid fishes, SMR varies several-fold among individuals within populations even after accounting for variation in body mass (Enders and Scruton 2005; Tyler and Buldoc 2008). Individual differences in SMR have important consequences for individual variation in energy acquisition, assimilation, and allocation (Bernardo and Reagan-Wallin 2002). There is a well-established positive effect of SMR on dominance rank within social hierarchies in stream salmonids (e.g., Metcalfe et al. 1995; Yamamoto et al. 1998; McCarthy 2001). In competition for feeding territories, fish with higher SMR tend to obtain stream positions with the highest rates of food delivery (Reid et al. 2011). This pattern has been observed in juvenile Atlantic salmon (*Salmo salar*) (Metcalfe et al. 1995), masu salmon (*O. masou*) (Yamamoto et al. 1998), and rainbow trout (*O. mykiss*) (McCarty 2001), suggesting a common relationship between SMR and competitive ability within salmonid fishes. Consequently, individuals with higher SMR tend to have higher rates of food acquisition because of the positive influence of SMR on competitive dominance.

Individual variation in SMR also influences the assimilation of food obtained from feeding territories. Generally, there is a tradeoff between SMR and assimilation efficiency that is mediated through gut residence time (Sibly 1981). Individuals with high SMR have shorter gut residence times and lower food conversion efficiency (Millidine et al. 2009), and consequently are expected to have lower energy assimilation for a given level of food acquisition.

SMR also influences the allocation of energy to competing functions. SMR limits the amount of residual energy available for storage, growth, and maturation after the

costs of maintenance have been met (Bernardo and Reagan-Wallin 2002). For a given rate of food acquisition, individuals with high levels of SMR have a lower amount of residual energy at their disposal, and this effect is compounded by the decrease in food assimilation efficiency associated with higher levels of SMR. Consequently, individuals with higher SMR must achieve a higher food acquisition rate in order to achieve a similar residual energy balance after accounting for energy loss due to higher costs of maintenance and lower assimilation efficiency.

The influence of SMR on all three components of resource economics suggests the potential for tradeoffs in energy acquisition, assimilation, and allocation strategies associated with individual variation in energy metabolism. The focus of my dissertation is the potential consequences of this physiological variation for the behavior and life histories of individuals in partially migratory populations of *O. mykiss*. In Chapter 2, I examine how individual variation in SMR in newly-emerged *O. mykiss* influences the acquisition of feeding territories across a gradient of intraspecific competition. I manipulated the intensity of intraspecific competition by stocking replicated laboratory stream channels at three levels of fish density while holding food and space constant. Within this context, I tested the hypothesis that competitive exclusion of subordinate fish, mediated through territorial behavior, results in density-dependent selection for higher SMR. In Chapter 3, I examine how variation in the spatial predictability of food resources influences the performance of newly-emerged *O. mykiss* with different physiological phenotypes in competition for food and space. I test the hypothesis that a decrease in the spatial predictability of food resources alters the influence of SMR on competitive

outcomes and has emergent consequences for population regulation. Results of Chapters 2 and 3 link individual variation in physiology, behavior, and viability during the critical transition from dependence on maternal provisioning of egg yolk reserves to the initiation of exogenous feeding. In Chapter 4, I examine potential carry-over effects of performance during early life stages on subsequent growth and developmental trajectories, including the expression of anadromous and freshwater-maturing phenotypes. Using behavioral assays, I separated a full-sibling cohort of steelhead offspring into competitively dominant and subordinate phenotypes and reared these groups of fish under two different temperature regimes until they demonstrated the outward expression of traits associated with anadromous and freshwater-maturing phenotypes. By tracking individual body size throughout the experiment, I determined how temperature, behavioral phenotypes, and individual growth trajectories influenced life-history expression. Chapter 5 integrates the results of these experiments. I conclude that manipulative experiments can help reveal the sometimes-cryptic processes influencing strategies for the acquisition and allocation of energy in species with complex life histories. Mechanistic approaches to the study of individual resource economics can improve the management and conservation of partially migratory salmonids, especially in light of the potential challenges imposed by global climate change.

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Chapter 2—Density-dependent selection on standard metabolic rate during early ontogeny in steelhead trout

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Abstract

Territorial animals can experience strong density-dependent mortality and displacement during initial stages of territory acquisition and defense. Individual variation in physiological traits such as standard metabolic rate (SMR) can influence competitive outcomes, but the effect of competitor density on the association between SMR and fitness is unclear. We determined the effect of conspecific density and individual variation in SMR (estimated from otolith microstructures) on territory acquisition by newly-emerged steelhead trout (*Oncorhynchus mykiss*) in laboratory stream channels stocked at three levels of population density (25, 75, and 100 fish·m^{-2}). Territory acquisition was positively associated with SMR across all treatments, but directional selection on SMR was strongest at intermediate stocking densities, moderate at the highest stocking densities, and weakest at lowest stocking densities. We found a strong correlation between rates of overt aggression and the strength of selection on SMR across all treatments, suggesting that competitive exclusion, mediated through agonistic behavior, was the mechanism driving patterns of selection on SMR. These results suggest a density-dependent link between intraspecific variation in physiology, behavior, and offspring viability during early ontogeny in territorial species. As one in a suite of bioenergetic factors influencing life-history traits during subsequent life stages, selection on SMR during early ontogeny may influence life-history trajectories in phenotypically plastic species.

Introduction

Mortality rates during early life stages can be extremely high in a wide variety of organisms, especially those with high fecundities. Offspring may be particularly vulnerable during their transition from dependence on maternally provisioned resources to the initiation of exogenous feeding (Sinclair 1989; Nislow et al. 2004; Armstrong and Nislow 2006). For species dependent on feeding territories, this transition marks the first expression of phenotypic traits associated with territory acquisition and defense (Kalleberg 1958; Dill 1977). Because density-dependent displacement and mortality can be severe during this critical period (sensu Elliot 1985; Nislow et al. 2004; Armstrong and Nislow 2006), phenotypic variation in traits influencing territory acquisition may provide an exceptional opportunity for selection, perhaps exceeding that of any subsequent life stage (Einum et al. 2004).

Energy metabolism is positively correlated with competitive dominance in many species (Careua et al. 2008; Biro and Stamps 2010). Metabolic rate could, therefore, be a trait under strong selection during early ontogeny when competition for food and space is intense. However, relatively few studies have examined selection on physiological traits. Recent studies demonstrate that energy metabolism is a repeatable trait in individuals and have stimulated increased interest in the association between fitness and standardized measures such as basal metabolic rate (BMR) and standard metabolic rate (SMR) (Hulbert and Else 2000). Both BMR and SMR are measures of the rate at which an animal burns calories to sustain basic physiological processes. (Strictly speaking, BMR refers to the energetic cost for endotherms at rest in a post-absorptive state while at thermoneutrality, while SMR refers to that for ectotherms in a post-absorptive, resting state. However, for simplicity, we hereafter use only the term SMR

to refer to the obligatory cost of maintenance in all taxa.) SMR has been shown to affect fitness in a wide variety of taxa, including mammals (e.g., Salesbury and Armitage 1995; Chappell et al. 2004; Gebczynski and Konarzewski 2009), birds (e.g., Bryant and Newton 1994; Mathot et al. 2009; Nilson et al. 2011), invertebrates (Brown et al. 2003; Artacho and Nespolo 2009), and fish (e.g., Metcalfe et al. 1995; Cutts et al. 1998; McCarthy 2001).

Natural selection should favor phenotypes that maximize the residual energy available for growth, survival, and reproduction (Sibly and Calow 1986; Brown et al. 1993; Kieser 1995). Higher maintenance costs might reduce the energy available for these competing functions and therefore reduce fitness, all things being equal. However, in some contexts SMR is positively correlated with behaviors that facilitate preferential access to food resources, resulting in a net increase in energy acquisition despite higher maintenance costs (Metcalfe et al. 1995; Reid et al. 2011). For example, intraspecific variation in SMR is often positively associated with boldness, aggression, and competitive dominance (reviewed in Careua et al. 2008, Biro and Stamps 2010, and Burton et al. 2012). Thus, individuals with faster metabolisms may be at an advantage in territorial contests for limited food and space. SMR may, therefore, be a trait under strong selection in territorial species during early ontogeny, and the strength of selection may depend on the density of intraspecific competitors. However, relatively few studies have examined links between SMR and territory acquisition under varying levels of intraspecific competition.

Stream-dwelling salmonid fish provide excellent models for investigating density-dependent links between SMR and fitness for a variety of reasons. Juvenile salmonids (called fry for the first 2 – 3 months after emergence from gravel redds) are highly territorial, expressing agonistic behaviors and establishing feeding territories within the first few days of stream life.

Adult fecundity is typically high relative to the availability of suitable rearing habitat, resulting in the potential for strong competition among fry for food and space (Chapman 1962; Elliot 1990). SMR is known to influence competitive ability in stream-rearing salmonids (e.g., Metcalfe et al. 1995; Cutts et al. 1998; McCarthy 2001) and SMR varies several-fold among individuals even after accounting for variation in body mass (Enders and Scruton 2005; Tyler and Buldoc 2008), providing ample opportunity for phenotypic selection during the initial stages of territory acquisition.

In this study, we determined the effect of conspecific density and individual differences in SMR on territory acquisition by juvenile *O. mykiss* during the transition from maternal provisioning to exogenous feeding. We manipulated the intensity of intraspecific competition by stocking replicated laboratory stream channels at three levels of fish density while holding food and space constant. Within this context, we tested the hypothesis that competitive exclusion, mediated through agonistic behavior, results in density-dependent selection on SMR. Our results link individual variation in physiology, behavior, and viability during this critical transition in salmonid life histories.

Materials and Methods

Study animals

We used a full-sibling cohort produced from anadromous steelhead parents from the Deschutes River, Oregon, USA for this experiment. Fish were obtained as fertilized eggs from Oregon Department of Fish and Wildlife's Round Butte Hatchery, and were the product of mating a single anadromous adult male and female captured at the Deschutes River Pelton Fish Trap. Immediately after fertilization, eyed eggs were transferred to Oregon State University's

(OSU) Salmon Disease Laboratory, Corvallis. Fish were incubated at 10°C until completion of yolk-sack absorption and the onset of exogenous feeding, at which point they were selected for inclusion in the experimental trials.

Experimental setup

We conducted the research in twelve experimental stream channels housed within OSU's Salmon Disease Laboratory. Experimental streams consisted of 2.4 m x 0.5 m rectangular channels with gravel substrate and a one-way fish emigration trap at the outflow. Water depth was a uniform 15 cm (Figure 2.1). Flow rate through the channels was approximately 2 $m^3 \cdot hr^{-1}$. Four 14 x 5 x 8 cm bricks were evenly spaced down the center of each stream to provide physical structure for fish orientation. We provided food to the experimental streams via automated belt feeders that dispensed 1.44 grams of Biodiet starter feed (Bioproducts, Warrenton, Oregon, USA) to the head of the channel over a 12 hr period beginning at 07:00 each day. Directional flow within the experimental streams distributed food throughout the channel. The amount of food supplied to each stream exceeded the maximum ration predicted by Marschall and Crowder's (1995) model for salmonids assuming a carrying capacity based on territory requirements for newly-emerged fish. Temperature within all streams was maintained at a constant 13°C. Photoperiod was held constant at 14 h light 10 h dark, a regime typical for the source population on the dates of the experiment. All streams were housed within an opaque plastic curtain to minimize disturbance to the study animals during the experiment.

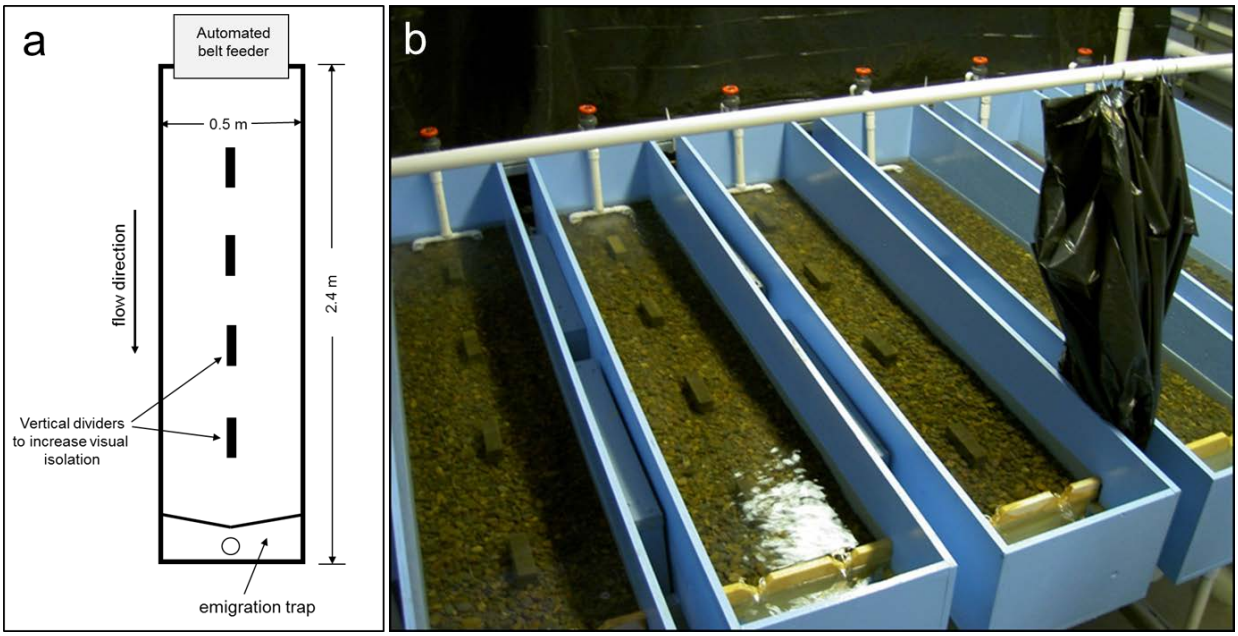

Figure 2.1. The layout of laboratory streams used to test the effects of density on selection for standard metabolic rate in juvenile *O. mykiss*. (a) Schematic diagram of the laboratory streams used in the experiment. (b) Photograph of a bank of six of the twelve streams at OSU Salmon Disease Laboratory.

To begin the experiment, we selected four groups each of 25, 75, or 100 fish, and randomly assigned each group to be stocked in one of the 12 experimental streams. During the 25 day experiment, we allowed fish to either establish territories within the streams or emigrate into the one-way fish trap. We monitored the emigration trap twice daily. We anesthetized and marked each fish with a small caudal fin clip upon their initial capture in the trap and returned them to the head of the stream channel after recovery from the anesthetic in order to prevent "accidental" emigration (Keeley 2001). If a marked fish was captured in the trap a second time, we removed it from the experiment, euthanized it by overexposure to buffered anesthetic (Finquel MS-222; Argent Chemical, Redmond, WA), and preserved the fish in 90% ethanol. We

performed piecewise linear regression (Hudson 1966) on the mean number of emigrants against the number of days since stocking to characterize temporal patterns of emigration. We constructed models with 2, 3, or 4 linear segments and selected the most parsimonious models using Akaike's information criterion, adjusted for small sample sizes (AIC_c), as recommended by Burnham and Anderson (2002). The model with the smallest AIC_c value was regarded as the most plausible, given the data, and models within two AIC_c units of the model with the lowest AIC_c value were considered to be equally supported by the data.

To examine the phenology of agonistic behavior and fish abundance, we performed behavioral observations of individual fish activity during the experiment. Behavioral observations were made from portals cut into the opaque curtain housing each stream channel in order to avoid disturbing the study animals. Agonistic activity is associated with territory establishment and defense (Chapman 1962; Hartman 1965) and includes behavioral signaling through fin extensions, gill flaring, and lateral displays, as well as overt aggression in the form of charges, chases, and attacks, as described for steelhead by Hartman (1965). We quantified rates of overt aggression using focal observations of individual fish within each stream (Martin and Bateson 1993). Rates of agonism were quantified by randomly choosing one fish per channel and counting agonistic encounters between that fish and any other fish over a period of 5 min between 10:00 and 12:00 hours on days 1, 5, and 18 of the experiment. These observation dates were selected to correspond to characteristic periods in salmonid population regulation that are driven by intraspecific interactions (e.g., Elliot 1990; Titus and Mosegaard 1991).

The experiment continued for a period of 25 days, by the end of which emigration from all stream channels had ceased for at least seven days. At the conclusion of the experiment, we

removed all remaining fish from the stream channels, euthanized them by overexposure to buffered anesthetic, and measured their fork length (FL) to the nearest 0.01 mm with a digital micrometer, and their wet weight to the nearest 0.01 g on an electronic balance. All fish were subsequently preserved in 90% ethanol.

Our examination of selection on SMR within experimental populations was facilitated by the analysis of fish otolith microstructures (Titus and Mosegaard 1991). In teleost fishes, otoliths are argonite ($CaCO_3$) structures of the inner ear whose growth is closely associated with fish metabolism (e.g., Wright 1991; Hüssy and Mosegaard 2004; Fablet et al. 2011). Circadian cycles of mineral accretion in otoliths result in permanent daily patterns of alternating opaque and translucent rings (Campana 1992; Fablet et al. 2011). Microstructural "checks" in otoliths are abrupt changes in the daily growth patterns that occur during life-stage transitions, characteristically at hatching and during the transition from maternal provisioning to exogenous feeding (referred to as "emergence" in salmonids because this transition marks the emergence of larvae from streambed gravel to the stream environment; Quinn 2005). Because otolith accretion is tightly coupled with fish metabolism (e.g., Wright 1991; Yamamoto et al. 1998), many researchers have used standardized otolith measurements at the time of emergence as a morphometric proxy for individual variation in SMR (e.g., Titus and Mosegaard 1991; Metcalfe et al. 1992; Bochdansky et al. 2005). The association between SMR and otolith size has been verified through strong correlations of otolith accretion rates and direct measurements of SMR in fish (Wright 1990; Yamamoto et al. 1998; Bang and Grønkjær 2005), as well as in mechanistic models of otolith biomineralization (Hüssy and Mosegaard 2004; Fablet et al. 2011).

To test the hypothesis that territory acquisition was related to SMR, we extracted sagittal otoliths from fish included in the experiment as well as from a separate sample of 25 fish from the same family that were not included in the experiment. The latter sample was used to examine correlations between otolith size and body size at the beginning of the experiment, because body size can also influence competitive asymmetries (e.g., Abbott and Dill 1985; but see Huntingford et al. 1990; Yamamoto et al. 1998). One sagittal otolith from each fish was mounted sulcus side up with a transparent adhesive (Crystal Bond 509) on a microscope slide. The otolith was ground with 2000-grit sandpaper and 0.05 μm alumina paste in the sagittal plane to reveal banding patterns, including the primordial core, nucleus, and the emergence check signifying the otolith size at the time of stocking into the experimental channels (Titus and Mosegaard 1991). We used a compound microscope and camera lucida to capture and import digital images of the polished otoliths into image analysis software (Image-Pro version 7.0). Otolith measurements were made from the posterior nucleus edge to the posterior edge of the emergence check along a fixed radius that was offset clockwise by 15º from the long axis of the otolith (Titus and Moosegard 1991).

We determined the effect of otolith size-at-emergence on territory acquisition by comparing otolith radius measurements of fish alive at the beginning of the experiment with those of fish that acquired and defended territories within the streams for the duration of the experiment. Because of the large number of individuals included in the experiment, and because some otoliths were damaged during removal and could not be analyzed, we measured otoliths from only a portion of the individuals that emigrated from or were retained within the experimental streams. We selected a random sample of at least 20% of all emigrating fish per day for otolith extraction, with replacements selected for individuals with damaged otoliths.

Because the numbers of otoliths suitable for measurement were disproportional to the respective numbers of emigrant and territorial fish, we weighted the mean and variance of otolith size for each stream to account for unmeasured individuals, as suggested by Blackenhorn et al. (1999).

We used two approaches for measuring the strength of selection on otolith size at emergence during the experiment. First, we calculated standardized selection differentials for each stream by taking the difference between the means of the otolith size at emergence of fish at the beginning of the experiment and those of fish that remained within the streams for the duration of the experiment. Selection differentials measure the net change in mean otolith size at emergence for populations over the course of the experiment and were standardized to units of phenotypic standard deviation by subtracting the mean value from each individual measurement and then dividing each value by the standard deviation of otolith size-at-emergence at the beginning of the experiment (Lande and Arnold 1983). We partitioned the total selection differential into distinct episodes by calculating conditional selection differentials (Lynch and Arnold 1988) for each experimental time period, as defined by piecewise linear regression of the mean daily number of stream emigrants over time. We also performed two sets of logistic regressions to determine the influence of variation in standardized otolith size at emergence on the probability of territory acquisition. For each stream replicate, fish that remained in the streams for the duration of the experiment were assigned a value of one, and emigrants were assigned a value of zero. We then estimated directional and quadratic selection on otolith size at emergence via two sets of regressions using the following statistical model (Lande and Arnold 1983; Stinchcombe et al. 2008):

$$\text{logit}\,(p) = \alpha + \beta_i\, z + \tfrac{1}{2}\gamma_i\, z^2 + \varepsilon_i,$$

where p is the probability of a fish remaining within a stream for the duration of the experiment, z is the standardized phenotypic value for otolith size at emergence, α is an intercept term, β_i is the directional selection coefficient, γ_i is the quadratic (nonlinear) selection coefficient, and ε_i is residual variation.

We performed two sets of logistic regression for each population (Carlson et al. 2008). In the first set, only the non-squared term for otolith size at emergence was used to estimate the relationship between otolith size at emergence and territory acquisition. In the second set, we used the full model, including squared values for otolith size at emergence, to the first set of regressions to estimate quadratic (nonlinear) influences on the probability of territory acquisition. Coefficients from these latter regressions are interpreted as representing stabilizing (when negative) or disruptive (when positive; Carlson et al. 2008) influences on territory acquisition.

Results

During the experiment, a drain malfunction resulted in the loss of fish from one of the streams stocked at low fish density, so we excluded data from this stream from subsequent analysis. We recovered 91% of the remaining 775 fish initially stocked into the channels, either by capture in the emigration trap or by removing them at the end of the experiment. We did not directly observe mortality within the stream channels during the experiment but the small number of unrecovered fish probably resulted from *in situ* mortalities that went undetected. The per capita rate of fish recovery did not vary among density treatments (overall mean ± SD = 91% ± 2%; $F_{2, 10} = 0.116$, $P = 0.892$).

Steelhead growth and behavior

Steelhead fry had a mean FL (±SD) of 28.59 ± 0.57 mm and mean mass (±SD) of 0.17 ± 0.014 at the beginning of the experiment. By the end of the experiment, steelhead that acquired territories within the stream channels had a mean FL (±SD) of 44.94 ± 3.13 mm and mean mass (±SD) of 1.03 ± 0.24 g. The mean change in body length is equivalent to an instantaneous growth rate of 1.81 $mm \cdot d^{-1}$ and a change in body mass equivalent to 0.17 $g \cdot d^{-1}$ Individual growth rate was not correlated with otolith size-at-emergence in any of the experimental streams ($|r| < 0.10$, $P > 0.05$ for all streams). Stocking density had no effect on final length or final fish mass for fish that remained within the experimental streams for the duration of the experiment (ANOVA, fork length, $F_{2,8} = 2.399$, $P = 0.153$; mass, $F_{2,8} = 0.547$, $P = 0.599$), or within-stream variation in final fish length or mass (ANOVA on gini coefficients, length, $F_{2,8} = 1.577$, $P = 0.265$; mass, $F_{2,8} = 1.176$, $P = 0.357$).

Emigration began within the first 24 h of the experiment. A three-segment piecewise linear regression dividing the experiment into three distinct periods was the most parsimonious model describing emigration rates in all density treatments, given the data, with alternative models of either 2 or 4 segments receiving little statistical support ($\Delta AIC_c > 20$). Period 1 was characterized by a rapid decrease in the number of fish retained within the streams (Figure 2.2), and spanned days 1 – 3 in all treatments (Table 2.1). Period 2 spanned days 3 – 11 (Table 2.1), and was characterized by moderate rates of emigration (Figure 2.2). The final period spanned days 9 – 25, and was characterized by relative population stability with low overall rates of emigration and no loss of fish for at least the last seven days of the experiment (Figure 2.2). The number of fish that remained within the experimental streams for the duration of the experiment

ranged from 7 to 16 fish·m^{-2}. The number of fish that remained within experimental streams varied among density treatments (ANOVA, $F_{2, 8} = 4.907$, $P = 0.041$), but significant differences were limited to contrasts between the low and high stocking density treatments (mean difference = 4.6 fish·m^{-2}; $P = 0.042$).

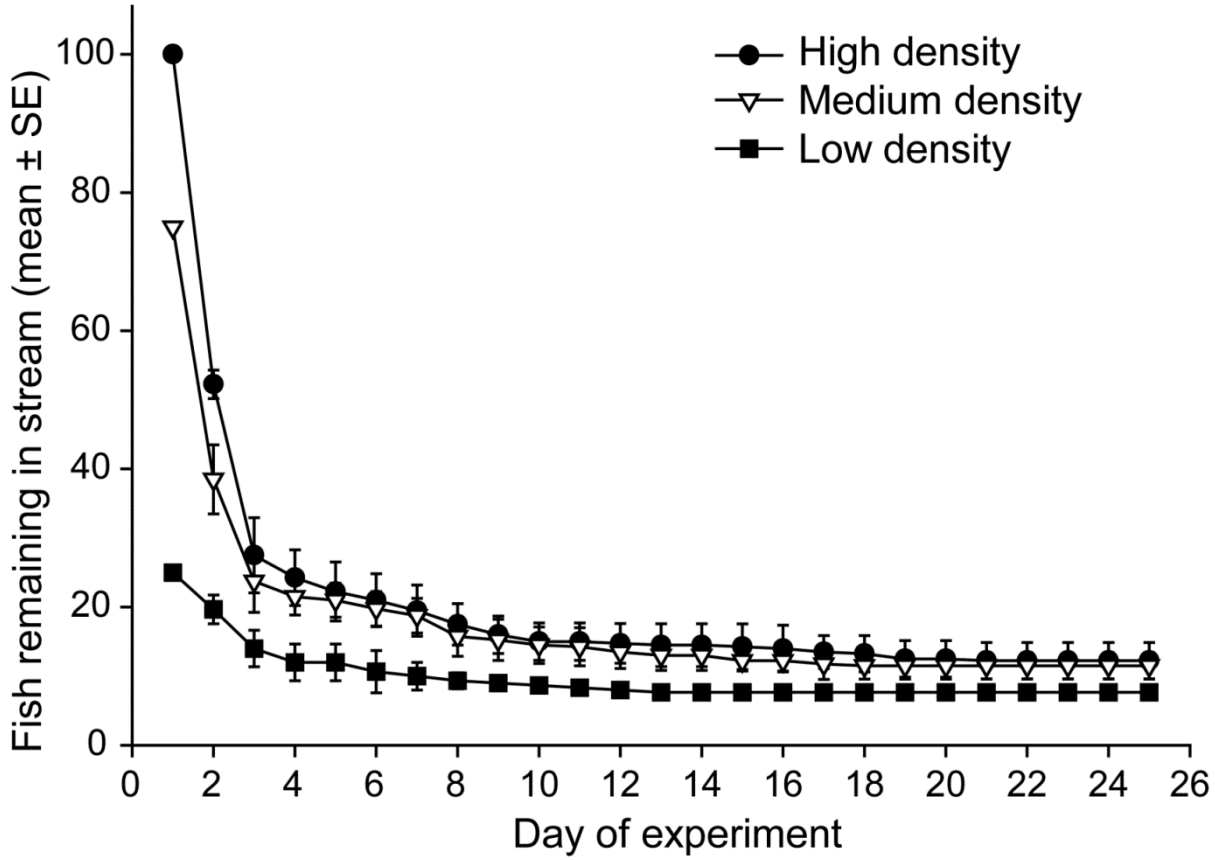

Figure 2.2. Mean daily number of steelhead fry remaining in experimental streams initially stocked at low (25 fish·m^{-2}), intermediate (75 fish·m^{-2}), and high (100 fish·m^{-2}) densities. Error bars represent ± 1 SE.

Agonistic behavior marking the initiation of competition for territories began in all experimental streams within the first day of the experiment. There was a significant interaction between stocking density and experimental period on rates of agonistic interactions (repeated measures ANOVA; $F_{3, 30} = 6.739$, $P = 0.003$). Within the low-density treatment, we observed the highest rates of agonism in periods 1 and 2, with significant reductions in agonism occurring between period 2 and period 3 ($P = 0.013$) (Figure 2.3). In the intermediate-density treatment, we observed significant reductions in agonism between each successive experimental period ($P < 0.05$ for all contrasts) (Figure 2.2). In the high-density treatment, rates of agonism were initially

Table 2.1. Mean emigration rate and duration of three periods of population regulation of juvenile steelhead trout estimated by piecewise linear regression of the number of emigrants leaving experimental streams on experimental day. Initial stocking densities were low (25 fish•m^{-2}), intermediate (75 fish•m^{-2}), and high (100 fish•m^{-2}). R^2 values are provided for each regression.

Density treatment	Emigration rate [fish·d^{-1}(SE)]			Final day of experimental period (SE)			
	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3*	R^2
low	3.8 (0.49)	0.6 (0.11)	0.1 (0.04)	3.3 (0.05)	11.4 (0.34)	25 (-)	0.98
medium	21.3 (0.65)	1.2 (0.24)	0.1 (0.06)	2.4 (0.02)	11.2 (0.41)	25 (-)	0.98
high	28.8 (0.78)	1.8 (0.34)	0.2 (0.03)	2.5 (0.02)	9.2 (0.22)	25 (-)	0.99

*The conclusion of the experiment on day 25 marked the end of period 3 in all streams.

low but increased significantly from period 1 to period 2 ($P = 0.003$), and then dropped significantly from period 2 to period 3 ($P = 0.003$). The low rates of aggression in the high density treatment during period 1 ran counter to the generally positive association between instantaneous fish density and agonistic interaction rate (Figure 2.3).

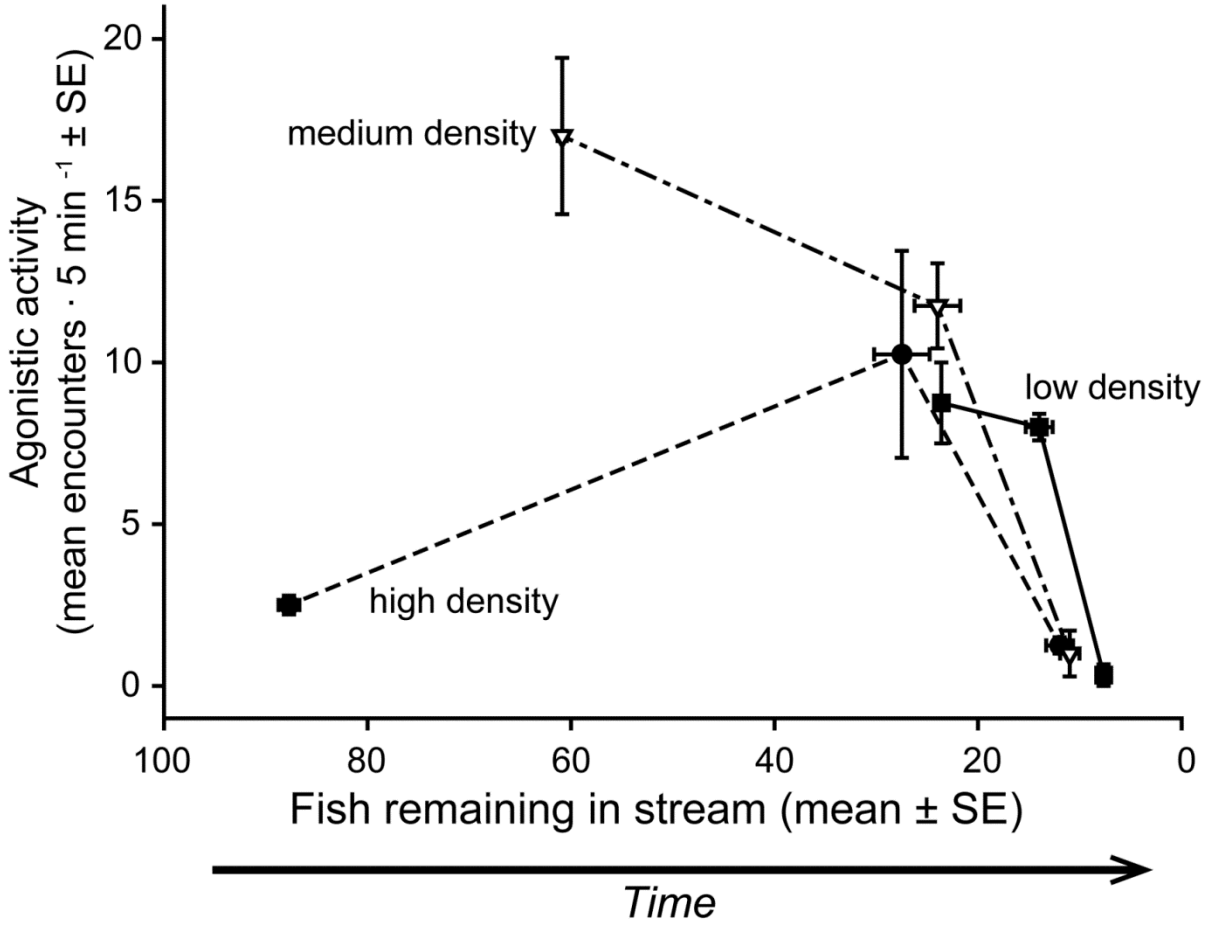

Figure 2.3. Mean per capita rate of agonistic activity in experimental streams initially stocked at low (25 fish·m^{-2}), intermediate (75 fish·m^{-2}), and high (100 fish·m^{-2}) densities. Lines connect values for behavioral observations made within each density treatment on days 1, 5, and 18 of the experiment in order of decreasing fish abundance, respectively. Error bars represent ± 1 SE.

Among the density treatments, we observed significant differences in the rates of agonism during period 1 (ANOVA; $F_{2, 10} = 21.217$, $P < 0.001$). Agonistic interaction peaked within the medium-density treatment at a mean rate of 3.4 interactions per minute, which was 2.9 ($P < 0.001$) and 1.65 ($P = 0.013$) interactions greater than in the high- and low-density treatments, respectively. During period 2, the overall mean rate of agonism was 2.0 interactions per minute and did not differ among the density treatments (ANOVA; $F_{2, 8} = 0.881$, $P = 0.447$). The overall mean rate of agonism decreased to 0.2 interactions per minute during period 3, with stocking density having no effect on agonistic rates (ANOVA; $F_{2, 8} = 0.805$, $P = 0.480$).

Steelhead otolith size at emergence and territory acquisition

Mean (± SD) steelhead otolith size at emergence was 160 ± 11 µm and was similar among the density treatments at the beginning of the experiment (ANOVA, $F_{2, 8} = 0.301$, $P = 0.748$). Otolith size was not associated with initial fish length or mass, when measured in a random selection of 25 steelhead from the same family included in the experiment (linear regression, length, $F_{1, 24} = 0.0514$, $P = 0.823$; mass, $F_{1, 24} = 1.54$, $P = 0.226$). Across all treatments, the average otolith size at emergence for steelhead acquiring territories (mean ± SD: 168 ± 41 µm) was 6% larger than that of emigrating steelhead (157 ± 12 µm; $t_{10} = 8.49$, $P< 0.001$). Standardized selection differentials for otolith size at emergence were positive, ranging from 0.43 to 1.34 units of phenotypic standard deviations greater the mean otolith size at emergence for the entire population at the beginning of the experiment (Table 2.2).

Stocking density had a significant effect on standardized selection differentials (ANOVA, $F_{2, 8} = 50.04$, $P < 0.001$), with the strongest selection occurring in the intermediate-density treatment, and the weakest selection occurring in the low stocking density treatment (Table 2.2).

Selection differentials in the low- density treatment were, on average, 0.62 standard deviations smaller than those in the medium density treatment ($P < 0.001$), and 0.37 standard deviations lower than the high density treatment ($P = 0.001$). Selection differentials in the high-density treatment were, on average, 0.25 standard deviations lower than in the medium-density treatment ($P = 0.006$). Temporal trends in selection among the density treatments indicated that selection

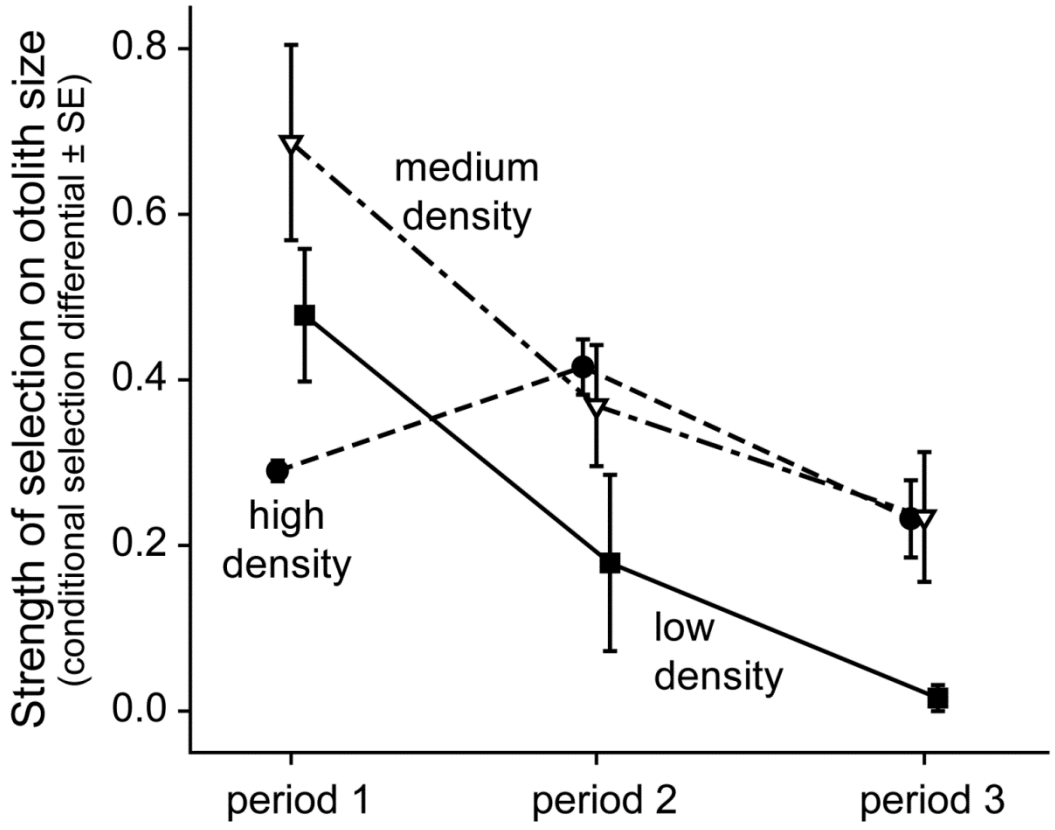

Figure 2.4. Temporal trends in the mean strength of selection on otolith size-at-emergence across three experimental periods in streams initially stocked at low (25 fish·m^{-2}), intermediate (75 fish·m^{-2}), and high (100 fish·m^{-2}) densities. Strength of selection refers to standardized selection differentials in units of standard deviations from a phenotypic mean of zero. Error bars represent ± 1 SE.

Table 2.2. Summary of analyses of selection acting on otolith size at emergence in juvenile steelhead trout stocked in experimental streams at low (25 fish·m^{-2}), intermediate (75 fish·m^{-2}), and high (100 fish·m^{-2}) densities. Directional (logistic) and quadratic (nonlinear) selection coefficients and standardized selection differentials are presented for replicate streams and data pooled across treatment replicates.

	Directional coefficients			Quadratic coefficients			Standardized selection differentials			
Density Treatment	β	SE	*P*	γ	SE	*P*	Period 1	Period 2	Period 3	Total
Low										
Stream 1	1.009	0.561	0.072	0.047	0.922	0.960	0.64	-0.03	0.00	0.61
Stream 2	1.174	0.595	0.048	-0.819	1.434	0.568	0.41	0.24	0.00	0.64
Stream 3	1.792	0.859	0.036	-0.316	1.642	0.847	0.39	0.33	0.05	0.76
Replicates pooled	1.261	0.370	<0.001	-0.153	0.670	0.820	0.48	0.18	0.02	0.67
Intermediate										
Stream 4	3.863	1.081	<0.001	0.147	3.274	0.964	0.41	0.52	0.30	1.23
Stream 5	3.361	1.366	0.008	1.679	2.145	0.434	0.85	0.45	0.00	1.30
Stream 6	3.067	0.824	<0.001	-2.387	2.159	0.269	0.91	0.18	0.31	1.40
Stream 7	3.008	0.830	<0.001	2.049	1.207	0.090	0.57	0.33	0.33	1.23
Replicates pooled	3.248	0.461	<0.001	0.469	1.121	0.676	0.69	0.37	0.23	1.29
High										
Stream 8	3.697	1.284	0.004	0.424	1.360	0.745	0.32	0.43	0.35	1.10
Stream 9	1.829	0.481	<0.001	0.301	0.812	0.711	0.27	0.58	0.17	1.02
Stream 10	2.034	0.596	<0.001	-0.209	1.478	0.888	0.29	0.55	0.27	1.11
Stream 11	1.431	0.492	0.003	0.279	0.771	0.717	0.27	0.52	0.14	0.93
Replicates pooled	1.853	0.284	<0.001	0.251	0.510	0.622	0.29	0.52	0.23	1.04

on otolith size at emergence in the low- and intermediate-density treatments was strongest during period 1 relative to subsequent experimental periods, while in the high--density treatment, selection was strongest during experimental period 2 (Figure 2.4). These patterns paralleled measures of overt aggression: across treatments and experimental periods the mean strength of selection on otolith size was strongly positively correlated with mean rates of overt aggression ($r = 0.84$, $P = 0.004$).

Consistent with selection differentials, the probability of acquiring a territory was positively associated with otolith size at emergence in all streams as indicated by directional selection coefficients (Table 2.2) (Figure 2.5). None of the quadratic selection coefficients were significantly different from zero, indicating that there was no evidence for stabilizing or disruptive selection on otolith size at emergence. On average, in the intermediate-density treatment, the odds of acquiring a territory increased 31% for every unit increase in standardized values for otolith size at emergence. This was 28% and 20% higher than the associated increase in odds of territory acquisition in the low- ($P = 0.032$) and high-density ($P = 0.05$) stocking treatments, respectively.

Discussion

During the initial stages of territory acquisition and defense, steelhead that successfully established territories had significantly larger otoliths at emergence than those that emigrated from experimental streams. This result is consistent with previous studies demonstrating a positive association between the size of an individual's otolith size at emergence and survival during the transition from maternal provisioning to exogenous feeding (West and Larkin 1987;

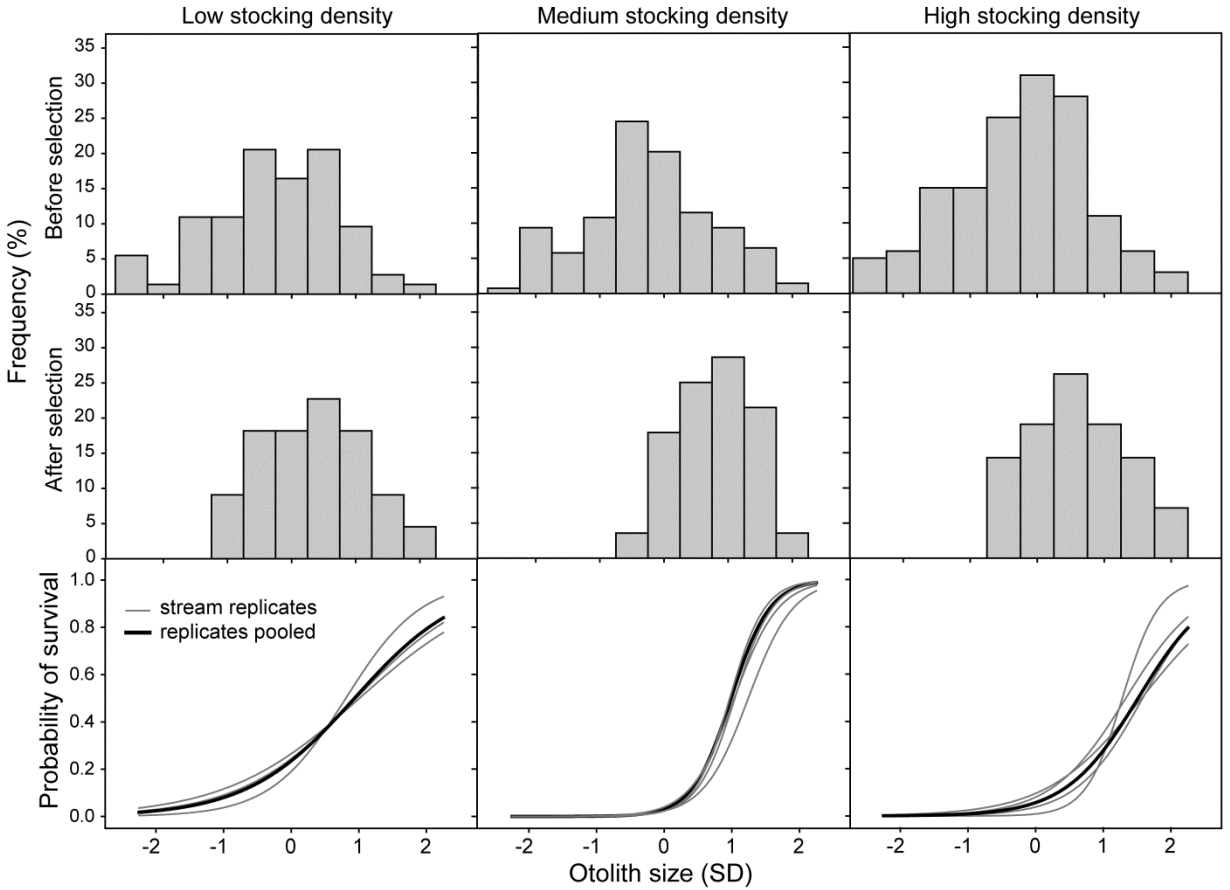

Figure 2.5. Frequency of standardized otolith size-at-emergence before (top row) and after (middle row) selection in experimental streams initially stocked at low (25 fish·m^{-2}), intermediate (75 fish·m^{-2}), and high (100 fish·m^{-2}) densities. The bottom row shows results from logistic regressions of the probability of territory acquisition as a function of standardized otolith size-at-emergence in units of standard deviations from a phenotypic mean of zero. Results from both replicated streams (gray lines) and data pooled across treatment replicates (bold black lines) are shown.

Mosegaard 1990; Titus and Mosegaard 1991). While our objective in this study was to gain insight into the relationship between salmonid viability and physiological variation, and not otolith size *per se*, the use of otolith size at emergence as a proxy for SMR enabled us to examine trait variation in a much larger number of individuals than would be possible using direct measurements of energy metabolism. The use of otolith structures as an index of relative metabolic status is well supported by previous research demonstrating that metabolic processes govern the rate of otolith accretion in teleosts (Wright 1991; Yamamoto et al. 1998; Bang and Grønkjær 2005).

In juvenile salmonids, the link between metabolic rate and otolith size is robust, as both Wright (1991) and Yamamoto et al. (1998) found that otolith accretion was strongly correlated (i.e., $r > 0.90$) with SMR in age-0 Atlantic salmon (*Salmo salar*) and masu salmon (*O. masou*), respectively. Because otolith accretion is directly influenced by energy metabolism, differences in otolith size at emergence reflect relative differences in metabolic rates among individuals (Titus and Mosegaard 1991; Bang and Grønkjær 2005). Thus, the relationship between otolith size and territory acquisition that we observed is likely driven by the well-established positive effect of SMR on competitive ability (e.g., Metcalfe et al. 1995; McCarthy 2001; Reid et al. 2011).

While previous research has demonstrated a positive influence of SMR on competitive ability, few experiments have examined how SMR and intraspecific density interact to determine the probability of territory acquisition. Recently, Reid et al. (2011) demonstrated experimentally that SMR was positively associated with dominance rank in small groups of 1-year-old Atlantic salmon, and that high-ranking fish were more likely to acquire high-quality feeding territories in

laboratory streams. In their study, the advantages of metabolic rate for acquiring a high-quality territory increased with increasing fish density. We observed the strongest selection on SMR at intermediate population densities. We found a strong correlation between overt aggression and selection on SMR across all treatments and experimental periods, suggesting that competitive exclusion, mediated through agonistic behavior, was the mechanism driving patterns of selection. We also observed the highest rates of aggression at intermediate fish densities, which explains why selection on SMR was strongest in streams receiving intermediate stocking densities.

These observations are consistent with previous theoretical and empirical investigations of resource defense by territorial animals (Keenleyside and Yamamoto 1962; Fenderson and Carpenter 1971; Brown et al. 1992). A central prediction of resource defense theory is that territorial behavior is adaptive when the energetic benefits of resource defense exceed the costs (Brown 1964). As competitor density increases, increased investment in territorial behavior remains economical until a threshold density is crossed, above which the energy expended attempting to monopolize resources exceeds the potential energetic gains (Grant 1993). Consequently, territory defense through agonistic behavior is expected to peak at intermediate animal densities, a pattern demonstrated by several other fish species (e.g., Keenleyside and Yamamoto 1962; Jones 1983; McNichol and Noakes 1984).

In our study, we assumed that the majority of emigrating fish had been competitively excluded from the stream channels. This assumption is consistent with our observations of agonistic behavior within the stream channels, and was also supported in a companion study in which emigrant and territorial steelhead were size-matched and placed in dyad trials in order to determine the relative competitive ability of the two types of fish (Chapter 4). In 20 of 25 (80%)

trials, fish that established territories in the experimental streams also were dominant over emigrants when allowed to contest food and space in size-matched dyads, confirming inferences about competitive dominance in larger groups within the experimental streams. The downstream dispersal of competitively subordinate salmonid fry is also commonly observed in both semi-natural (e.g., Chapman 1962; Titus and Mosegaard 1991; Keeley 2001) and natural streams (e.g., Elliot 1984; Bujold et al. 2002; Westley et al. 2008).

Downstream-emigrating fry face an uncertain future. It is possible that some emigrants would survive if they encountered empty rearing space (Elliot 1986; Titus and Mosegaard 1991). For example, estuarine rearing by downstream migrating fry occurs in coho salmon (*O. kisutch*) (Koski 2008), a species with territorial behavior similar to steelhead (Hartman 1965). However, this life history is not known to occur in steelhead or other anadromous salmonids with extended freshwater rearing (e.g., brown trout [*Salmo trutta*], Atlantic salmon). Generally, emigrating salmonid fry are thought to have very high rates of mortality because they are commonly moribund, ill, or in poorer condition than fish that acquire territories, and are more vulnerable to predation than sedentary fry (e.g., Elliot 1984; Bujold et al. 2002; Westley et al. 2008). Consequently, stream-rearing salmonid fry are generally expected to have limited ability to successfully disperse from areas of high intraspecific density upon emergence (Einum et al. 2006).

The energetic consequences of selection on SMR during early ontogeny are likely to reverberate throughout subsequent life stages. Standard metabolic rate is a repeatable trait in individuals of many species (recently reviewed by Nespolo and Franco 2007, Biro and Stamps 2011, and Burton et al. 2011), so that individuals possessing relatively high metabolic rates

during early life stages are also likely to have relatively high metabolic rates later in life (e.g., McCarthy 2000; O'Connor et al. 2000; Cutts et al. 2001). While individuals with relatively high metabolic rates may benefit from improved competitive ability, through which they may obtain better feeding territories, this benefit is held in tension against the higher maintenance costs. One such cost is a reduction in growth efficiency. For example, Reid et al. (2011) demonstrated that while Atlantic salmon with faster metabolic rates are more likely to obtain a high-quality feeding territory, their growth is poorer on a given territory than that of fish with slower metabolisms. Similarly, Alvarez and Nicieza (2005) observed neutral or negative relationships between individual SMR and growth in wild populations of brown trout. So, while metabolic rate may be positively associated with the acquisition of high-quality feeding territories, this does not necessarily translate into improved growth. These observations may help explain the lack of correlation between fish otolith size at emergence and somatic growth within our experiment.

The effect of metabolic rate on growth rate and growth efficiency is likely to influence additional components of fitness, since these bioenergetic parameters underlie critical life-history traits such as the occurrence and timing of ontogenetic habitat shifts and the size and age at reproduction (Forseth et al. 1995; Morineville and Rasmussen 2003). The implications of selection on metabolic rate are particularly relevant for life-history expression in partially migratory species whose populations consist of alternative migratory phenotypes. In partially migratory salmonid populations, fish with higher metabolic expenditures during juvenile rearing are more likely to adopt anadromous life histories than they are to forego migration and complete their life cycle in freshwater (Forseth et al. 1995; Morineville and Rasmussen 2003). Consequently, strong directional selection for individuals with faster metabolic rates, mediated

through intense competition for feeding territories during early ontogeny, may produce a correlated response in which more individuals are likely to adopt migratory behavior (e.g., anadromy) at later life stages. Weaker selection on metabolic rate may result in a greater diversity of physiologies within a surviving cohort when juvenile competition is low, which may produce a greater mix of alternative migratory phenotypes. The result, at the population level, is that the strength of selection on metabolic rate during early ontogeny may be one proximate mechanism influencing the diversity of life histories expressed within salmonid cohorts.

If true, this hypothesis suggests the potential for positive feedbacks between population demography, physiology, and life-history expression in partially migratory species. Fecundity scales exponentially with body mass, and anadromous females are commonly an order of magnitude larger at maturity than their resident counterparts (Quinn 2005). Due to the high fecundity of large anadromous females, juveniles are more likely to encounter initially high competitor densities in streams with anadromous spawners than in streams supporting non-migratory populations (e.g., Elliot 1994; Morita et al. 2000; Bohlin et al. 2001). Therefore, if intense juvenile competition favors fast-metabolism phenotypes, and these phenotypes are bioenergetically predisposed to anadromy, the high fecundity of anadromous females is likely to perpetuate intermediate or high juvenile densities, which should reinforce the premium on fast-metabolism phenotypes in subsequent generations.

Under such positive feedbacks, we would expect that populations in which juveniles consistently experience intense competition for feeding territories would exhibit higher values for traits related to territoriality. The magnitude and direction of selection on SMR that we observed during territory acquisition suggest the possibility for a relatively rapid evolutionary

response even under low levels of heritability in SMR. Although comparisons among populations are rare, this prediction has some support from previous studies. Lahti et al. (2001) demonstrated through a common-garden experiment that juvenile brown trout originating from anadromous populations had higher rates of aggression than those originating from resident populations, and Lahti et al. (2002) later found that overt aggression and standard metabolic rate were almost perfectly correlated (r = 0.99) within a subset of those populations. Although he did not measure metabolic differences among life-history types, Zimmerman (2000) used a common-garden approach to demonstrate that offspring of anadromous steelhead from the Deschutes River, Oregon had higher rates of aggression than rainbow trout offspring from the same basin. Similarly, Kristensen and Closs (2007) found higher levels of aggression in offspring from migratory brown trout experiencing very high juvenile densities than in offspring from a parapatric resident population with relatively low juvenile densities in the same river basin. Rosenau and McPhail (1987) also demonstrated experimentally that juvenile coho salmon from a high-density population were more aggressive and became dominant over those from a neighboring low-density population.

While our results and previous studies suggest the potential for adaptive shifts toward higher SMR and correlated behavioral traits (e.g., aggression; Lahti et al. 2002; Biro and Stamps 2010) in populations experiencing high densities during juvenile stages, our use of otolith size-at-emergence as an index of relative SMR adds some uncertainty to our conclusions about the relationship between SMR and fitness. The genetic covariance between these traits has yet to be explored, although phenotypic correlations between otolith size-at-emergence and SMR may exceed 0.90 (Wright 1991; Yamamoto et al. 1998). Therefore, the selection differentials we

measured apply strictly to the changes in trait means for otolith size-at-emergence and not SMR, per se. In addition, our experiment in semi-natural laboratory streams omitted some of the complexities of natural environments that may moderate the benefits of high SMR. For example, Hoogenboom et al. (2012) demonstrated that a decrease in the spatial and temporal predictability of food resources reduced the fitness benefit of high SMR in juvenile brown trout. The presence of predators may also offset the fitness advantages of a high SMR if individuals with high SMR also exhibit riskier behavior under conditions of food limitation (Killen et al. 2011). These factors suggest the possibility that the strength of selection on SMR may be reduced within more complex ecological settings.

Despite these limitations, our results demonstrate that the transition from dependence on maternal provisioning of food resources to exogenous feeding can produce an episode of strong selection on physiological traits in territorial salmonids. The correlation between rates of overt aggression and the strength of selection suggests that competitive exclusion, mediated through agonistic interactions, provides the most likely mechanism for selection on energy metabolism that we observed. Selection acting on energy metabolism may also lend insight into the expression of life-history traits in phenotypically plastic species for which conditional strategies depend on individual energy allocation strategies. Due to the association between energy metabolism and migratory behavior in other salmonid species (Forseth et al. 1995; Morineville and Rasmusen 2003), selection on SMR, mediated through resource defense, may also influence life histories for a wide variety of species.

Acknowledgements

We thank Don Ratliff, Rich Madden, and Jack Palmer for help obtaining fish for this experiment. Brian Nielsen and India Sloat helped with the construction of the experimental streams. Jerri Bartholomew and Don Stevens provided access to the OSU's Salmon Disease Lab. Special thanks to Don Stevens for his assistance with fish rearing and experimental setup. Mike Reeves extracted and polished hundreds of otoliths. Funding for this work was provided by the USDA Pacific Northwest Research Station and the Oregon American Fisheries Society Carl Bond Memorial Scholarship. The use of animals in this experiment was conducted under OSU Animal Care and Use Permit # 3923 and 4019.

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Chapter 3—Demographic and phenotypic responses of juvenile steelhead trout to variation in the spatial predictability of food resources

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Abstract

We manipulated food inputs among patches in experimental streams to determine the demographic and phenotypic responses of steelhead trout (*Oncorhynchus mykiss*) to the spatial predictability of food resources. Demographic responses of experimental populations to decreasing spatial predictability of food resources included compensatory adjustments in fish abundance, mean fish size, and size inequality. These responses resulted from shifts in individual foraging behavior that changed the form of intraspecific competition from primarily interference competition in streams with spatially predictable food resources to a mixture of scramble and interference competition in streams with spatially unpredictable resources. Streams with different levels of spatial predictability of food resources also favored different physiological phenotypes. We observed positive directional selection for individuals with faster rates of energy metabolism in spatially predictable streams, disruptive selection for energy metabolism in intermediate streams, and negative directional selection for energy metabolism in streams with the lowest level of spatial predictability of food resources. Thus, variation in the spatial predictability of food resources resulted in changes in individual behavior and modes of population regulation, and produced physiologically divergent populations.

Introduction

Modes of social interaction among individuals can strongly influence the mechanisms of population dispersion and regulation (e.g., Wynne-Edwards 1959; Fretwell 1972; Łomnicki 1988). When food and space are limiting, population responses depend on the tactics that individual animals use to exploit these resources. The spatial and temporal distribution of resources strongly influences behavioral choices of individual animals and, therefore, variation in these components of habitat structure should have consequences for behaviorallymediated demographic processes (Levin et al. 2000).

The spatial predictability of resources is a key component of habitat structure that also influences individual behavior (e.g., Brown 1969; Grand and Grant 1994; Grant 1993). In a heterogeneous environment, spatial predictability is a measure of the dependability of relative habitat patch quality over time (Warner 1980). When food resources are spatially predictable, competitively dominant individuals can effectively monopolize food resources through aggression and territoriality (Brown 1969; Grant 1993). Territoriality may act to regulate population size through density-dependent mortality, emigration, and growth in spatially heterogeneous but temporally static environments (e.g., Chapman 1966; Elliot 1990; Keeley 2001). In many environments resources are not static, however, and habitat patch quality may vary substantially over time (Martin-Smith and Armstrong 2002). A prediction of resource defense theory is that aggressive defense of feeding territories should produce an energy deficit when the spatial predictability of food resources falls below a critical threshold (Brown 1969; Grant 1993). Under such conditions, animals with flexible foraging strategies may abandon territoriality in favor of foraging tactics that minimize energy expenditure. Such an

environmentally-induced shift in foraging behavior may alter population responses to food and space competition. Consequently, mechanisms of population regulation may vary along gradients in the spatial predictability of food resources.

Variation in the spatial predictability of food resources may also exert different selective pressures on populations in addition to inducing individual behavioral changes. In populations experiencing predictable food regimes, traits that improve an individual's ability to monopolize access to food are likely to be favored. Individual variation in energy metabolism is a potentially important trait in this regard, as standard metabolic rate (SMR) is positively associated with boldness, aggression, and competitive dominance in a wide range of taxa (reviewed in Careua et al. 2008, Biro and Stamps 2010, and Burton et al. 2012). Thus, individuals with faster rates of energy metabolism may be at an advantage in territorial contests for limited food and space when resources are economically defendable (sensu Brown 1969). In environments with low spatial predictability in food resources, however, individuals with lower SMR may be favored if low maintenance costs help minimize energy loss during periods of food scarcity (Bochdansky et al. 2005). SMR may, therefore, be a trait under strong selection in response to the spatial predictability of food resources.

In this study, we conducted an experiment to test how spatial predictability of food resources influences behavior and early demography in a stream-dwelling salmonid and how the performance of individuals is influenced by variation in SMR. We studied offspring of steelhead trout (*Oncorhynchus mykiss*), the anadromous form of rainbow trout (Behnke 2002). This species is a good candidate for such a study because juvenile salmonids have flexible foraging strategies, which include both aggressive competition for feeding territories and non-territorial strategies

(e.g., “floaters”, sensu Pucket and Dill 1985). Additionally, SMR varies several-fold among individuals within populations even after accounting for variation in body mass (Enders and Scruton 2005; Tyler and Buldoc 2008), and SMR is known to influence dominance under interference competition in salmonids (e.g., Metcalfe 1995; McCarthy 2001; Reid et al. 2011). Consequently, there is strong potential for phenotypic selection on energy metabolism within populations due to variation in SMR, and a functional relationship between SMR and individual performance. To manipulate the spatial predictability of food resources within replicated experimental streams, we created habitat patches that received one of three levels of food input, and then varied the dependability of patch quality over time. By monitoring how individual phenotypes and demographic characteristics responded to levels of spatial predictability of food resources, we examined how individual variation in physiology and behavior contribute to changes in abundance, growth, and emigration in populations of stream-dwelling salmonids.

Materials and Methods

Collection and rearing of experimental animals

A full-sibling group of steelhead fry from the Siletz River, Oregon was used in the experiment. Fish were obtained as eggs by mating a single male and female of first-generation Siletz River winter steelhead hatchery stock. Oregon Department of Fish and Wildlife maintains this stock using 100% wild broodstock from the Siletz River to minimize genetic effects of domestication. Eggs were incubated at 10ºC at the Oregon Hatchery Research Center, Alsea, OR and transferred to Oregon State University’s Salmon Disease Laboratory, Corvallis, as alevins just prior to completing egg yolk absorption. All fish were kept in a single 100 L tank until yolk absorption was complete and they were ready to feed exogenously.

Experimental design

We constructed twelve artificial stream channels housed at OSU's Salmon Disease Laboratory. Each stream consisted of a 2.4 m x 0.5 m rectangular channel with gravel substrate and a one-way fish emigration trap at the outflow (Figure 3.1). Flow rate through the channels was approximately 2 $m^3 \cdot hr^{-1}$ and water depth was a uniform 15 cm. Three 14 x 5 x 8 cm bricks were evenly spaced within each stream to provide physical structure for fish orientation. Temperature was maintained at a constant of 13°C among all streams. Photoperiod was held constant at 14 h light 10 h dark, a regime typical for the source population at the time of the experiment. All streams were housed within an opaque plastic curtain to minimize disturbance to the study animals.

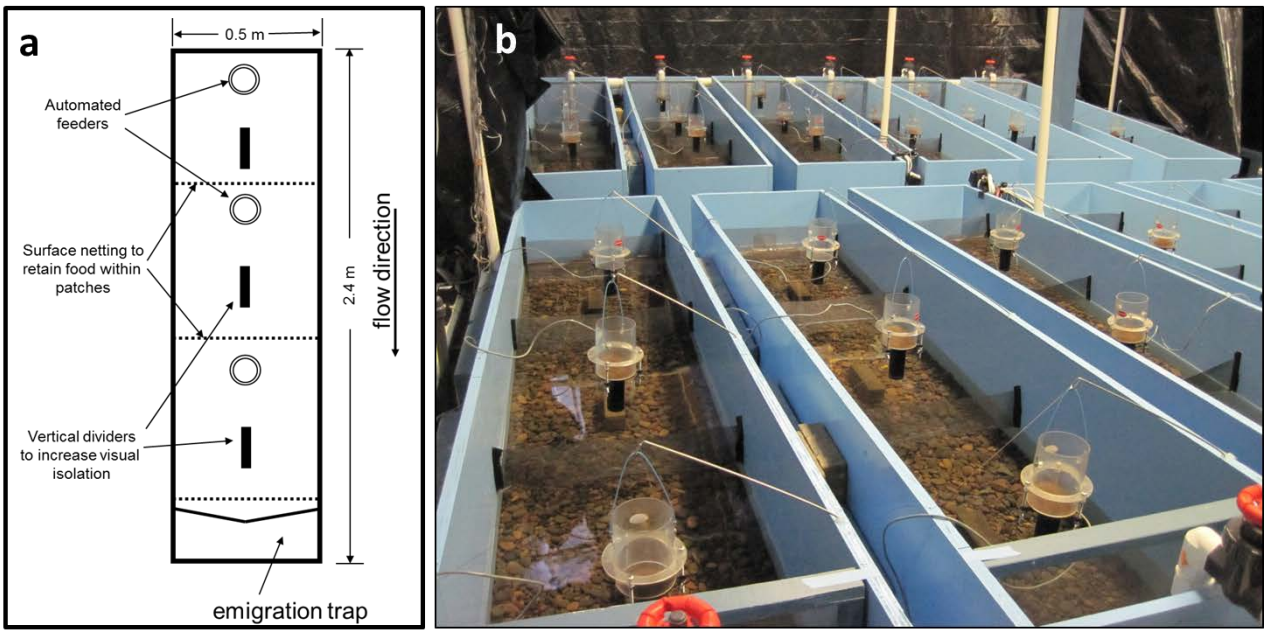


Figure 3.1. The layout of laboratory streams used to test the effects of spatial predictability of food resources on selection for standard metabolic rate in juvenile *O. mykiss.* (a) Schematic diagram of the laboratory streams used in the experiment. (b) Photograph of the twelve stream channels at OSU Salmon Disease Laboratory.

Each stream was divided into three feeding patches of equal size that received high, medium, or low amounts of food (Figure 3.1). Food, in the form of floating flakes (BioDiet starter feed, Bioproducts, Warrenton, Oregon, USA), was delivered to feeding patches by automated jitter feeders that dispensed food at pre-programmed time intervals. We created feeding patches by securing 1-mm-mesh nylon netting that extended 5 mm beneath the water surface perpendicular to the stream channel. The netting retained food within each feeding patch while allowing fish to swim freely between patches. Jitter feeders dispensed an equal amount of food per feeding (mean ± SE = 0.06 g ± 0.009). Differences in the daily quantity of food delivered to each feeding patch were controlled by the number of food dispensations per day. High food abundance patches received a total of 0.72 grams of feed over 12 feedings per day, medium food abundance patches received a total 0.30 grams over five feedings per day, and low food abundance patches received a total of 0.18 grams over three feedings per day, for a total food delivery to each stream of 1.2 $g \cdot d^{-1}$.

While an equal amount of food was delivered to each stream channel per day, streams differed in the spatial predictability of feeding patch quality. Four streams each were assigned one of three levels of spatial predictability in feeding patch quality. The spatial arrangement of patch quality (i.e., patches of high, medium, or low food abundance) remained constant throughout the experiment in the high predictability treatment. Patch quality changed every three days in the medium predictability treatment. Patch quality changed daily in the low predictability treatment (Figure 3.2).

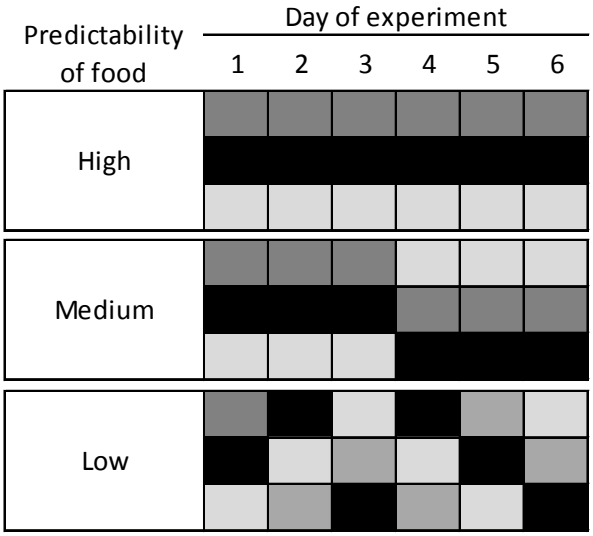


Figure 3.2. An example of the experimental feeding regimes used to manipulate the spatial predictability of food resources. Each shaded square represents a feeding patch receiving high (black squares), medium (dark gray squares), or low (light gray squares) levels of food input. Under the high spatial predictability treatment, the distribution of patch quality was constant throughout the experiment. Under the medium spatial predictability treatment, patch quality was randomly changed every three days. Under the low spatial predictability treatment, patch quality was randomly changed every day. An example of spatial arrangements of food patch quality is shown for the first six days of the 22-day experiment.

To begin the study, we selected 12 groups of 60 steelhead trout and then randomly assigned each group to an experimental stream. This level of stocking represented three to four times the carrying capacity for juvenile steelhead trout, based on previous studies using the same experimental system. Stream channels were opened to emigration after an acclimation period of four days. During the acclimation period, fish in streams with low spatial predictability in patch quality had experienced four changes in patch quality, those in streams with medium spatial predictability had experienced one change in patch quality, and those in highly predictable streams experienced none. Emigration was allowed into a one-way fish trap at the downstream end of each stream channel. We emptied the emigration trap twice daily to monitor emigration

rates. To prevent “accidental” emigration, we anesthetized and marked each fish with a small caudal fin clip upon their initial capture in the trap and returned them to the head of the stream channel after recovery from anesthesia (Keeley 2001). If a marked fish was captured in the trap a second time, we removed it from the experiment, euthanized it by overexposure to buffered anesthetic (Finquel MS-222; Argent Chemical, Redmond, WA), and preserved the fish in 90% ethanol. At the end of the 22-day experiment, I removed all remaining steelhead from the experimental channels, euthanized them, and measured their fork length (FL) to the nearest mm and their wet weight to the nearest 0.01 g.

We examined the spatial distribution of fish that remained within the experimental streams every three days using scan observations to count the number of fish per patch in each stream. Three observations were made on each observation day, during which we estimated the number of stationary fish (i.e., fish remaining within a feeding territory during the observation) within each food patch as well as the number of mobile fish per stream. We also performed focal animal observations at three-day intervals. During focal observations, we categorized fish into behavioral types based on their foraging tactics. Territorial fish maintained one or two nearby focal positions from which they made short forays to feed or interact with other fish and to which they consistently returned. Floaters (sensu Pucket and Dill 1985) were fish that rarely remained stationary, moved among feeding patches within the experimental streams, and fed while freely swimming. Focal animals were observed to determine feeding and agonistic rates for territorial fish and floaters. Fish were observed for 3 min and each feeding and agonistic event was mapped. To facilitate mapping of behavioral events, we embedded a matrix of white marbles on the stream substrate and used the matrix as well as the location of a single brick placed in the

center of each stream patch as visual reference points. We then made scaled planform drawings of the experimental streams, dividing each stream into 5 cm x 5 cm cells and using the marbles and bricks as reference points. During behavioral observations, we mapped focal positions as well as the location of feeding or agonistic events at the grain (i.e., minimum mapping unit) of the 5 cm x 5 cm cells. Territory size was calculated as the number of cells defended during observation multiplied by the area of each cell (i.e., 25 cm^2). We made similar 3-min observations of floaters, except that these fish did not occupy focal positions. All behavioral observations were made from portals cut into the opaque curtain housing each stream channel in order to avoid disturbing the study animals.

Our examination of selection on SMR within experimental populations was facilitated by the analysis of fish otolith microstructures (Titus and Mosegaard 1991). In teleost fishes, otoliths are argonite ($CaCO_3$) structures of the inner ear in which growth is closely associated with fish metabolism (e.g., Wright 1991; Hüssy and Mosegaard 2004; Fablet et al. 2011). Circadian cycles of mineral accretion in otoliths result in permanent daily patterns of alternating opaque and translucent rings (Campana 1992; Fablet et al. 2011). Microstructural “checks” in otoliths are abrupt changes in the daily growth patterns that occur during life-stage transitions, characteristically at hatching and during the transition from maternal provisioning to exogenous feeding (referred to as “emergence” in salmonids because this transition marks the emergence of larvae from streambed gravel to the stream environment; Quinn 2005). Because otolith accretion is tightly coupled with fish metabolism (e.g., Wright 1991; Yamamoto et al. 1998), many researchers have used standardized otolith measurements at the time of emergence as a morphometric proxy for individual variation in SMR (e.g., Titus and Mosegaard 1991; Metcalfe

et al. 1992; Bochdansky et al. 2005). The association between SMR and otolith size has been verified through strong correlations of otolith accretion rates and direct measurements of SMR in fish (Wright 1990; Yamamoto et al. 1998; Bang and Grønkjær 2005), as well as in mechanistic models of otolith biomineralization (Hüssy and Mosegaard 2004; Fablet et al. 2011).

Before we stocked fish in experimental streams, otoliths of all fish were marked with alizarin complexone to facilitate easy identification of otolith size at the beginning of the experiment. Fish were submerged for four hours in an aerated bath of 50 $mg \cdot l^{-1}$ alizarin complexone buffered by KOH and then allowed to recover for 6 hours. No mortality was observed during marking. To examine individual variation in otolith size at emergence, we extracted sagittal otoliths from both emigrant fish and fish that remained within the channel for the entire experiment. One sagittal otolith from each fish was mounted sulcus side down using a transparent adhesive (Crystal Bond 509) on a microscope slide. The otolith was ground with 2000-grit sandpaper and 0.05 μm alumina paste in the sagittal plane to reveal banding patterns, including the alizarin complexone mark signifying the otolith size at the time of stocking into the experimental channels. We used a compound microscope and camera lucida to capture and import digital images of the polished otoliths into image analysis software (Image-Pro version 7.0). The total area within the emergence check, delineated by the alizarin complexone mark, was measured to determine individual variation in otolith size at emergence.

Data Analysis

We used repeated-measures analyses of variance (ANOVAR) to assess the effects of spatial predictability of food resources on the demography of juvenile *O. mykiss* held in the stream channels. When responses were measured on a specific group of fish at only a single

point during the experiment, such as for those fish that were removed at the end of the experiment, we used univariate analysis of variance (ANOVA) to assess treatment effects. To quantify the degree of size inequality in a population, we used the relative mean size difference between all pairs of individuals (Gini coefficient; Weiner and Solbrig 1984; Keeley 2001).

We compared otolith area measurements of all fish alive at the beginning of the experiment with those of fish that were retained within the streams for the duration of the experiment (Lande and Arnold 1983) to determine the effect of otolith size at emergence on the probability of fish remaining within experimental streams. For each stream, otolith size was standardized by subtracting the mean value from each individual measurement, and then dividing by the standard deviation of otolith size at emergence for the population at the beginning of the experiment (Lande and Arnold 1983). We used two approaches for measuring the strength of selection on otolith size during the experiment. First, we calculated standardized selection differentials for each stream by taking the difference between the means of the otolith size at emergence of fish at the beginning of the experiment and those of fish retained within the streams for the duration of the experiment. Selection differentials measure the net change in mean otolith size for the experimental populations as a result of selection (Lande and Arnold 1983). We also performed logistic regressions to determine the influence of variance in standardize otolith size on fish retention within the experimental streams. For each stream replicate, fish that were retained in the streams for the duration of the experiment were assigned a value of one, and emigrants were assigned a value of zero. We then estimated directional and quadratic selection on otolith size at emergence via two sets of regressions using the following statistical model (Lande and Arnold 1983; Stinchcombe et al. 2008):

$$\text{logit}(p) = \alpha + \beta_i z + \tfrac{1}{2}\gamma_i z^2 + \varepsilon,$$

where p is the probability of a fish remaining within a stream (either zero or one, as defined earlier), z is the standardized phenotypic value for otolith size at emergence, α is an intercept term, β_i is the directional selection coefficient, γ_i is the quadratic (nonlinear) selection coefficient, and ε is residual variation.

We performed two sets of logistic regression for each population (Carlson et al. 2008). In the first set, only the non-squared term for otolith size at emergence was used to estimate logistic selection differentials, which represent the total strength of selection acting on otolith size at emergence. In the second set, we used the full model including squared values for otolith size at emergence to the first set of regressions to estimate quadratic (nonlinear) selection differentials. Coefficients from these latter regressions are interpreted as representing stabilizing selection (when negative) or disruptive selection (when positive; Carlson et al. 2008).

Lastly, we complemented parametric statistical analyses of phenotypic selection by performing univariate cubic splines (nonparametric regressions) to visualize the form of selection acting on each population (Schluter 1988). We generated by these splines using general additive models fit by generalized cross-validation using the program R (R development core team 2009).

Results

Of the 720 fish initially stocked into the channels at the beginning of the experiment, we were able to recover 99% of these individuals either as emigrants or by removing them at the end of the experiment. We did not observe any mortality within the stream channels during the

experiment, but the small number of unrecovered fish probably resulted from in situ mortalities that went undetected.

Numbers of fish within the streams declined through emigration over time in all treatments (ANOVAR, $F_{11, 73} = 641.696$, $P < 0.001$), but showed the largest and most rapid declines in the predictable treatment (Figure 3.3). The magnitude of treatment differences was greatest during days 6 through 12 of the experiment (Figure 3.3). Hence, there was an interaction of time × treatment on fish abundance (ANOVAR, $F_{2, 81} = 6.142$, $P < 0.001$). Experimental populations took fewer days to reach stable levels of abundance in streams with increasing predictability in feeding patch quality (ANOVA, $F_{2, 9} = 11.945$, $P = 0.003$; Figure 3.3). The number of fish remaining in a stream channel at the end of the experiment ranged from 22 – 31, and decreased with increasing predictability in feeding patch quality (ANOVA, $F_{2, 9} = 19.820$, $P < 0.001$; Figure 3.3). On average, predictable streams supported 14% and 24% fewer fish at the end of the experiment than streams with intermediate ($P = .029$) or low predictability in food patch quality ($P < 0.001$), respectively.

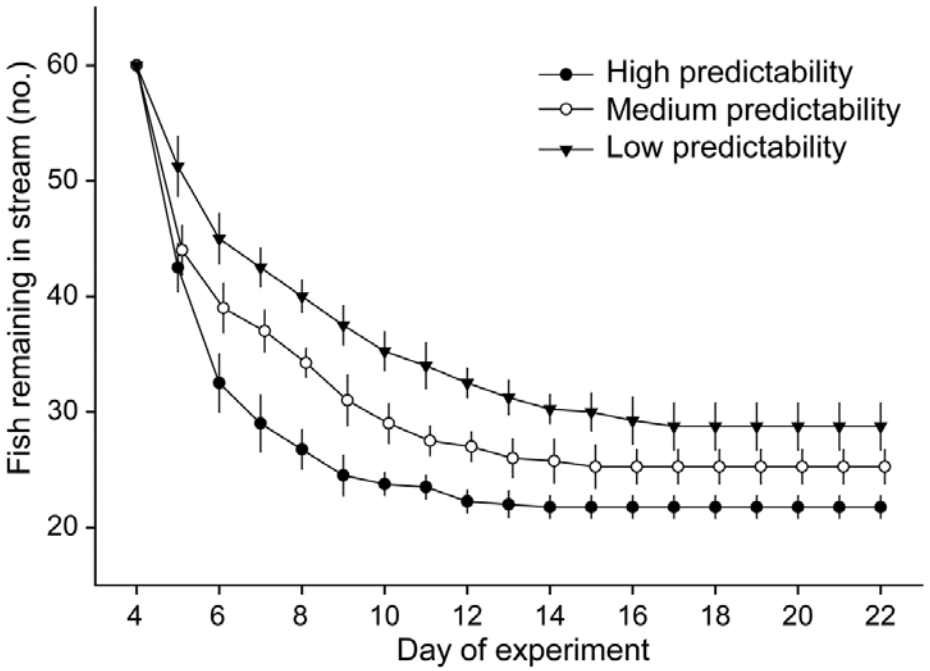


Figure 3.3. Mean daily number of juvenile steelhead remaining in experimental streams with high, medium, or low levels of spatial predictability of food resources. Error bars represent ± 1 SE.

Foraging behavior

During the experiment, fish adopted either territorial or floater foraging tactics (Pucket and Dill 1985; Nielsen 1992). Territorial fish typically maintained a single focal position from which they made short forays to feed or interact with other fish and to which they consistently returned. Floaters seldom remained stationary, moving nearly constantly throughout the experimental streams. Spatial predictability of food-patch quality influenced the proportion of fish adopting territorial versus floater foraging tactics within each stream (ANOVAR on arcsine-transformed proportions, $F_{2,81} = 95.111$, $P < 0.001$). With increasing spatial predictability of food, a higher proportion of fish held feeding territories, and the magnitude of the differences

increased over time, giving rise to a significant treatment × time interaction (ANOVAR, $F_{2,81}$ = 6.559, $P < 0.001$; Figure 3.4).

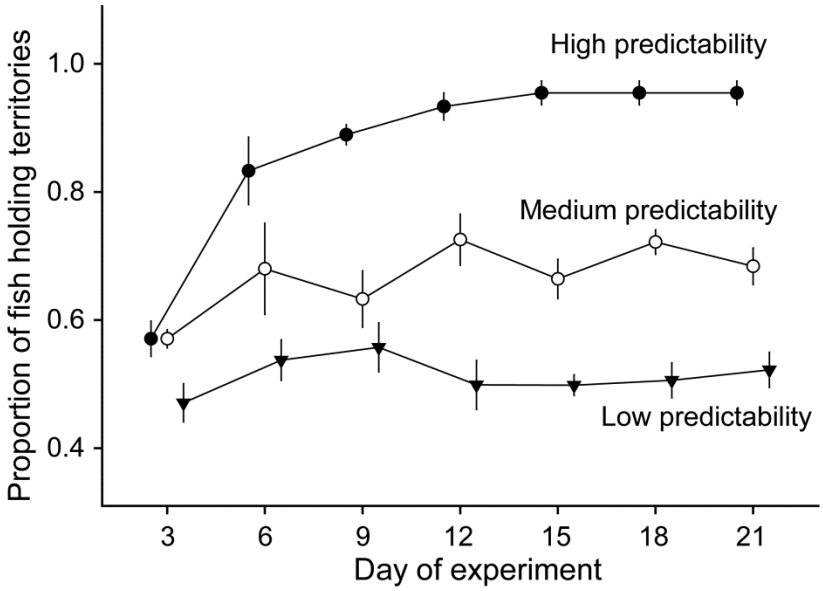


Figure 3.4. Mean proportion of juvenile steelhead populations holding territories in experimental streams with high, medium, or low levels of spatial predictability of food resources. Error bars represent ± 1 SE.

For fish acquiring territories, mean territory size increased over time in all streams (ANOVAR, $F_{6, 64} = 37.127$, $P < 0.001$), with no effect of treatment (ANOVAR, $F_{2, 70} = 0.567$, $P = 0.580$) and no interaction of treatment × time (ANOVAR, $F_{6, 64} = 0.796$, $P = 0.552$) on the increase in territory size. In streams with spatially predictable food resources, territory size was smaller in patches with higher food inputs (ANOVAR, $F_{2, 70} = 5.604$, $P = 0.026$; Figure 3.5) but the magnitude of these differences did not increase over time and therefore did not produce time × patch-quality interactions (ANOVAR, $F_{6, 64} = 0.892$, $P = 0.560$). In streams with intermediate or low spatial predictability of food resources, there was no association between the amount of food delivered to a patch and territory size (ANOVAR, intermediate predictability, $F_{2, 70} = 0.433$, $P = 0.662$; low predictability, $F_{2, 70} = 0.880$, $P = 0.448$; Figure 3.5).

In all treatments, territory holders had, on average, significantly higher food intake rates than floaters (Paired *t*-tests, high predictability, $t_6 = 4.285$, $P = 0.005$; medium predictability, $t_6 = 7.413$, $P < 0.001$; low predictability, $t_6 = 3.727$, $P = 0.010$; Figure 3.6). The difference between territory holders and floaters in mean food intake rates was greatest in streams with high spatial predictability of food resources (mean difference ± 95% Confidence Interval [C.I.] = 2.07 ± 1.18), and smallest in streams with the lowest spatial predictability (mean difference ± 95% C.I. = 0.69 ± 0.45). Within foraging behavior types, treatment had a significant effect on food intake rates, with territory holders having higher intake rates, on average, when the spatial predictability of food resources was higher (ANOVAR, $F_{2, 70} = 14.695$, $P = 0.001$; Figure 3.6). Floaters had significantly higher mean food intake rates as the spatial predictability of food resources decreased (ANOVAR, $F_{2, 70} = 6.509$, $P = 0.018$; Figure 3.6).

Territory holders and floaters also differed in their rates of agonistic interactions (Figure 3.6). In all treatments, territory holders had significantly fewer agonistic interactions, on average, than floaters (Paired *t*-tests, high predictability, $t = 13.830$, $P < 0.001$; medium predictability, $t = 5.786$, $P = 0.001$; low predictability, $t = 4.209$, $P = 0.006$; Figure 3.6). The difference in mean agonistic rates between territory holders and floaters was greatest in streams with high spatial predictability of food resources (mean difference ± 95% C.I. = 5.42 ± 0.92), and smallest in streams with the lowest spatial predictability of food resources (mean difference ± 95% C.I. = 2.05 ± 1.19). Differences between behavioral types in the direction of agonism were also apparent, as across all treatments floaters were the recipients of attacks in 92% of their agonistic

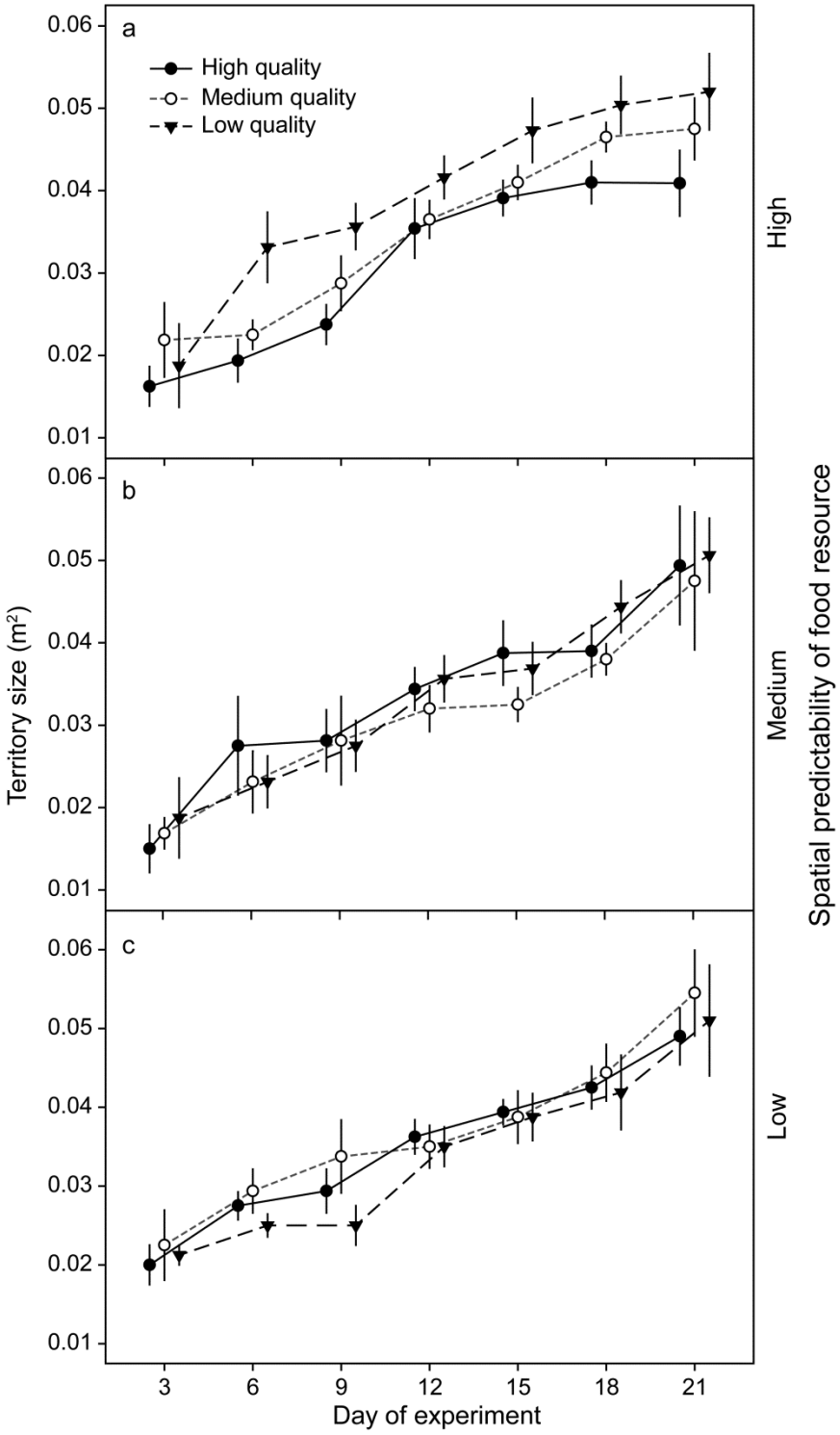


Figure 3.5. Mean territory size for juvenile steelhead populations occupying high, medium, or low quality food patches in experimental streams with (a) high, (b) medium, or (c) low levels of spatial predictability of food resources. Error bars represent ± 1 SE.

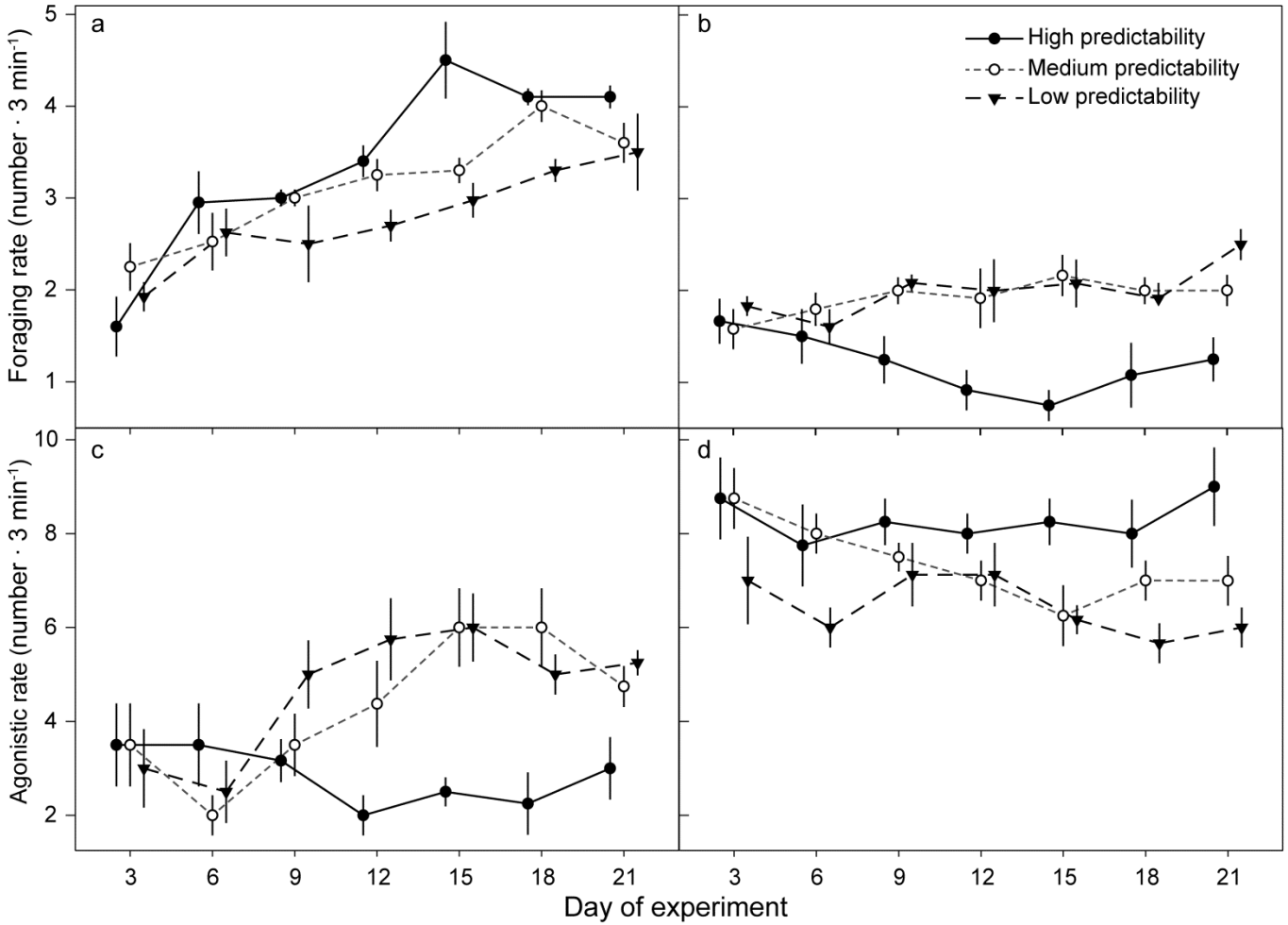


Figure 3.6. Foraging rates for (a) territory holders and (b) floaters, and agonistic rates for (c) territory holders and (d) floaters in streams with high, medium, and low levels of spatial predictability of food resources.

interactions, while territorial fish were aggressors in 84% of their agonistic interactions. Within foraging behavior types, treatment had a significant effect on agonistic rates, with territory holders having higher agonistic rates, on average, when the spatial predictability of food resources was lower (ANOVAR, $F_{2, 70} = 7.816$, $P = 0.011$; Figure 3.6). On average, floaters had significantly higher agonistic rates as the spatial predictability of food resources increased (ANOVAR, $F_{2, 70} = 12.450$, $P = 0.003$; Figure 3.6).

Fish size

Growth of fish within the stream channels was also affected by the spatial predictability of food resources. For fish retained within the stream channels until the end of the experiment, mean fish length (± S.D.) was 42.4 (± 2.5) and mean fish mass was 0.71 g (± 0.15). Mean fish length increased with increasing spatial predictability of food delivery (ANOVA, $F_{2, 9} = 15.76$, $P = 0.001$). Fish in streams with spatially predictable food resources were on average 6.4% (95% C.I: 1.3 – 8.0) and 3.5% (95% C.I.: 0.9 – 4.6) longer than fish in streams where food resources had intermediate or low spatial predictability, respectively. In addition to treatment effects on mean values, length frequency distributions showed different strengths of growth depensation at different levels in the spatial predictability of food resources (ANOVA, $F_{2, 9} = 13.833$, $P = 0.002$; Figure 3.7). Gini coefficients for length peaked in streams with intermediate spatial predictability and were lowest in streams with high spatial predictability of food resources (Figure 3.7). We also detected treatment effects on mean fish mass (ANOVA, $F_{2,9} = 6.34$, $P = 0.019$), but significant differences were restricted to contrasts between the high and intermediate food resource predictability treatments ($P = 0.020$). Variation in fish mass, as measured by Gini

coefficients, also peaked under the intermediate treatment and was lowest in streams with highest spatial predictability of food resources (ANOVA, $F_{2, 9} = 15.59$, $P = 0.001$; Figure 3.7). Total biomass per stream ranged from 21.0 $g \cdot m^{-2}$ to 14.8 $g \cdot m^{-2}$, with treatment having no effect on mean biomass (ANOVA,$F_{2, 9} = 0.084$, $P = 0.919$).

Selection on otolith size at emergence

Otolith size at emergence and body size at emergence were not significantly related (Linear regression, $F_{1, 26} = 3.339$, $P = 0.080$). Logistic regression analysis of the relationship between otolith size at emergence and the probability of an individual remaining within a stream for the duration of the experiment revealed both directional and nonlinear selection acting on this trait (Table 3.1). The nature of selection varied among treatments. In the spatially predictable treatment, directional selection was positive in all stream replicates, indicating that individuals possessing larger otoliths at emergence experienced greater survival, on average. Quadratic (nonlinear) coefficients were consistently positive, suggesting some selective loss of individuals with intermediate values of otolith size at emergence (Table 3.1). While the latter result suggested weak disruptive selection on this trait when food resources were spatially predictable, quadratic coefficients only approached statistical significance in formal analyses of selection when data from replicate streams were pooled (Table 3.1).

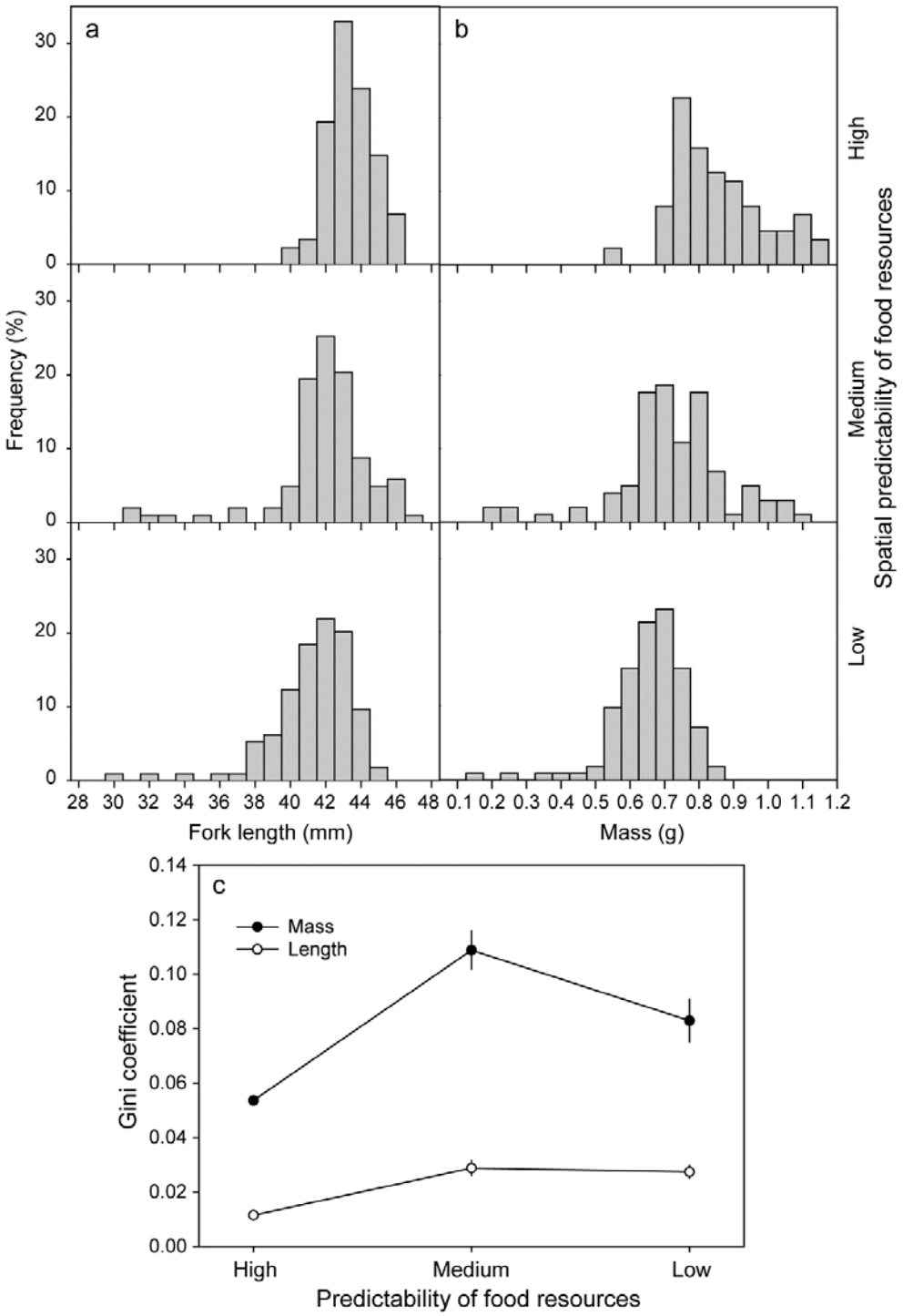


Figure 3.7. (a) Final length and (b) final mass frequencies for juvenile steelhead retained within streams with high, medium, and low levels of spatial predictability of food resources. (c) Mean Gini coefficients for length and mass frequency distributions in (a) and (b). Error bars represent ± 1 SE.

In contrast to patterns of selection under the spatially predictable treatment, directional selection in streams with low spatial predictability in food resources was consistently negative, indicating a survival advantage, on average, for individuals that possessed smaller otoliths at emergence (Table 3.1). Quadratic coefficients were a mix of positive and negative values among streams with low predictability of food resources, with none significantly deviating from zero (Table 3.1).

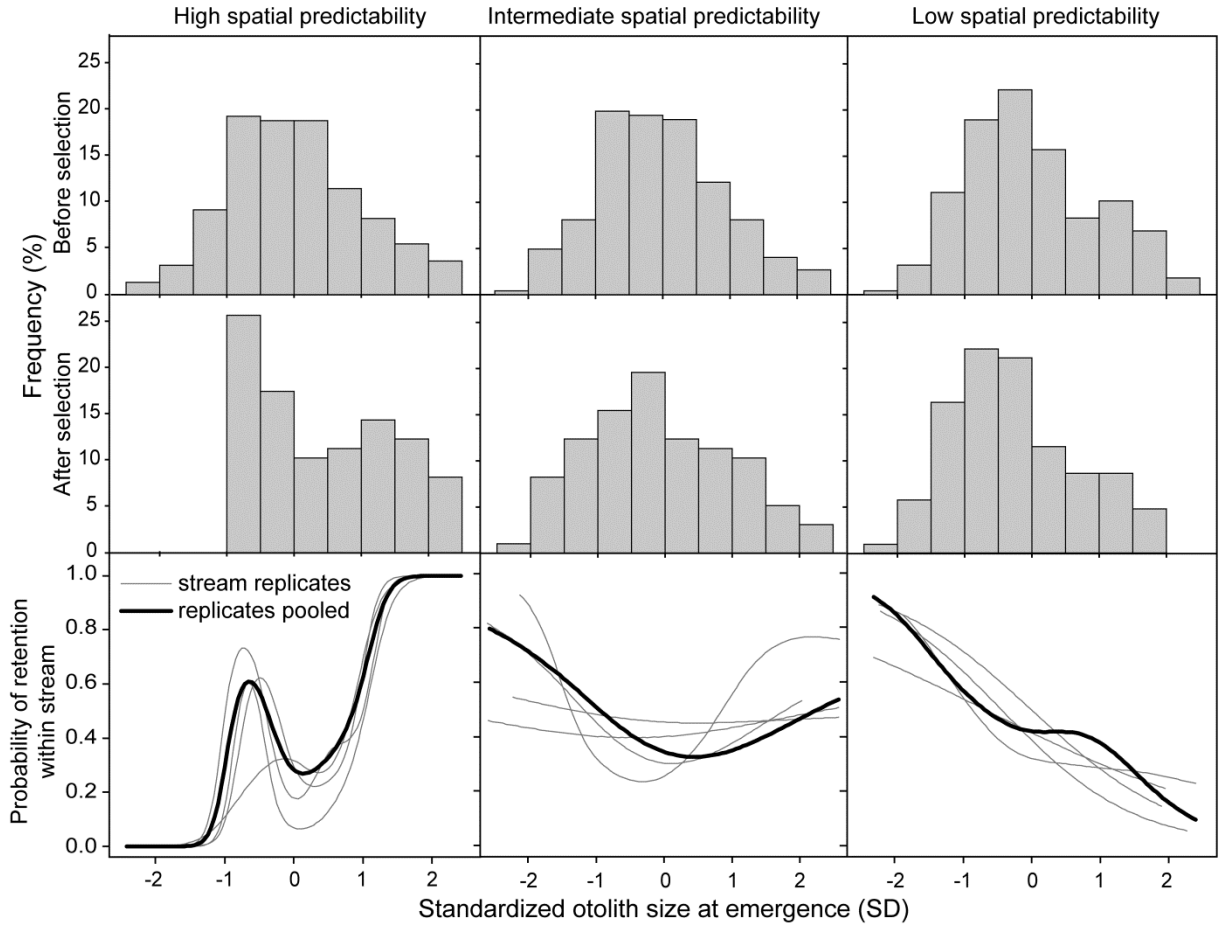
In streams intermediate in the spatial predictability of food resources, directional coefficients were a mix of positive and negative values, with none deviating significantly from zero. However, quadratic coefficients were consistently positive and statistically significant in two of the four streams, suggesting higher than average survival for individuals with relatively small or large otoliths at emergence in streams with intermediate food resource predictability (Table 3.1).

Visualization of selection surfaces with cubic spline plots confirmed overall patterns of directional and quadratic selection on otolith size at emergence identified by logistic regression (Figure 3.8). Selection on otolith size at emergence was positively directional and possibly disruptive in streams with high spatial predictability in food resources (Figure 3.8). In streams with low spatial predictability of food resources, selection surfaces were directional, consistently negative, and showed little evidence for either disruptive or stabilizing selection. In streams with intermediate spatial predictability, selection on otolith size at emergence showed little directionality but demonstrated evidence for disruptive selection (Figure 3.8).

Table 3.1. Summary of analyses of selection acting on otolith size at emergence in juvenile steelhead trout stocked in experimental streams with varying levels of temporal predictability of food resources. Directional (logistic) and quadratic (nonlinear) selection coefficients and standardized selection differentials are presented for replicate streams and data pooled across treatment replicates.

	Directional coefficients			Quadratic coefficients			Standardized
Density Treatment	β	SE	*P*	γ	SE	*P*	selection differentials
Predictable							
Stream B	0.797	0.330	0.016	0.407	0.510	0.424	0.39
Stream E	1.564	0.490	0.001	0.714	0.861	0.407	0.71
Stream G	2.303	0.318	0.009	0.901	0.725	0.214	0.48
Stream I	1.104	0.365	0.002	0.386	0.587	0.510	0.51
Replicates pooled	1.020	0.179	<0.001	0.542	0.299	0.070	*mean* = 0.52
Intermediate							
Stream D	0.082	0.275	0.785	0.139	0.417	0.763	0.05
Stream F	0.028	0.267	0.918	1.440	0.570	0.012	0.02
Stream H	-0.354	0.296	0.232	0.201	0.443	0.650	-0.19
Stream K	-0.240	0.278	0.389	1.162	0.570	0.041	-0.13
Replicates pooled	-0.113	0.138	0.412	0.682	0.230	0.003	*mean* = -0.04
Unpredictable							
Stream A	-1.204	0.300	0.006	-0.101	0.614	0.869	-0.43
Stream C	-0.495	0.289	0.087	0.105	0.497	0.833	-0.25
Stream J	-0.674	0.319	0.034	0.817	0.536	0.127	-0.33
Stream L	-0.766	0.309	0.026	0.097	0.665	0.884	-0.33
Replicates pooled	-0.717	0.162	<0.001	0.231	0.277	0.404	*mean* =-0.34

Figure 3.8. Frequency of standardized otolith size at emergence for steelhead populations at the beginning (top row) and end (middle row) of an experiment in streams with high, medium, and low levels of spatial predictability of food resources. The bottom row shows results from cubic spline analysis of the probability of fish retention within experimental streams as a function of standardized otolith size at emergence in units of standard deviations from a phenotypic mean of zero. Results from both replicated streams (gray lines) and data pooled across treatment replicates (bold black lines) are shown.



Energetic consequences of physiological variation

Because of the relatively small numbers of fish retained within each channel (Figure 3.3), we pooled data from streams within each treatment to examine correlations between otolith size at emergence and individual fish growth. Significant correlations between fish growth and otolith size at emergence were limited to streams with high spatial predictability of food resources, where otolith size at emergence was moderately and positively correlated with both final fish length and mass (n = 88; length, $r = 0.295$, $P = 0.005$; mass, $r = 0.275$, $P = 0.010$).

Discussion

Although individual behavior has long been thought to influence ecological processes that regulate populations (e.g., Wynne-Edwards 1959; Fretwell 1972; Łomnicki 1988), empirical work on the mechanistic linkages between behavioral and population ecology has lagged behind theory (Anholt 1997; but see Anholt 1990; Levin et al. 2000). In stream salmonids, studies linking behavior and population dynamics have focused on the influence of competition for feeding territories on density-dependent mortality, growth, and emigration (e.g., Chapman 1966; Elliot 1994; Keeley 2001). However, stream salmonids inhabit dynamic ecosystems, and individuals exhibit considerable behavioral flexibility in response to variation in the constraints of food and space (e.g., Pucket and Dill 1985; Nielsen 1994; Hoogenboom et al. 2012). Our study provides one of the first tests of the effects of spatial predictability of food resources on population regulation in salmonids or, to our knowledge, in any animal population.

In response to a decrease in the spatial predictability of food, juvenile *O. mykiss* exhibited different foraging tactics. Nearly all fish retained within predictable streams established feeding territories that they defended through agonistic interactions with neighboring territory holders. In

streams with intermediate or low spatial predictability of food resources, fewer fish held territories, and approximately one-third to one-half of the experimental populations foraged as floaters that ranged among feeding patches. The decreased dependence on feeding territories with decreasing predictability in food resources is expected under the economic defendability hypothesis (Brown 1969; Grant 1993): as input rates to a feeding patch become less predictable, the potential benefits of energy spent aggressively defending a territory are less certain. With decreasing predictability in the spatial distribution of food inputs, there were likely fewer territories of sufficient quality to provide a net energetic benefit to resource defense.

The reduction in territoriality among juvenile *O. mykiss* experiencing decreased spatial predictability of food resources may represent an environmentally-induced shift in the relative strengths of interference and scramble competition within experimental populations. Because behavioral interactions can be an integral component of population demography (Levin et al. 2000), a shift in form of intraspecific competition should result in changes in the modes of population regulation. In spatially predictable streams, steelhead populations were regulated to stable densities primarily through interference competition for feeding territories and selective emigration of subordinate individuals. Territory size became progressively smaller in patches with higher food inputs, resulting in increased local fish densities in higher-quality patches. Consequently, the distribution of fish among patches within predictable streams was consistent with the food input-matching expectations of the ideal despotic distribution model (Fretwell 1972). An apparent outcome of matching within-patch fish abundance to food quantity was an increase in the mean size and a decrease in size inequality of steelhead in predictable streams relative to streams with a lower spatial predictability of food resources. Thus, despite a four-fold

difference in the quality of feeding patches within streams, fish size was normalized through patch-specific adjustments in territory size and fish abundance when the spatial distribution of patch quality was predictable.

Streams with lower predictability in the spatial distribution of food resources supported, on average, a greater number of smaller fish. Since food and space exert complementary controls on stream salmonid populations (Keeley 2001), the increased prevalence of floaters and decreased proportion of territory holders may have facilitated higher fish abundance in streams with lower predictability of food resources by relaxing the constraints of space on abundance. For example, floaters were less likely to be attacked by territory holders in streams with lower spatial predictability of food resources, suggesting that there was more undefended space available for floaters to exploit in these streams. Thus, even while the total input of food remained constant across treatments, streams with lower spatial predictability of food resources supported higher fish densities due to the reduced intensity of interference competition for space.

The increased abundance of fish in streams with lower spatial predictability of food resources was matched by a compensatory reduction in mean fish size and an increase in size inequality among individuals. Several factors may have contributed to the reduction in mean fish size. Reduced growth is a common density-dependent response to increased abundance in stream salmonids (e.g., Jenkins et al. 1999; Keeley 2001; Imre et al. 2005), and the reduction in mean size could be a result of partitioning a limited amount of food resources among a greater number of individuals. Correlations between within-patch fish abundance and patch quality were also much weaker in streams with lower spatial predictability of food resources than in spatially predictable streams. Thus, on average, more fish than expected under an IDD model were

present in low-quality feeding patches, and this mismatching of patch-specific fish abundance and food quantity could contribute to a decrease in mean fish size. Lastly, and perhaps most importantly, the increased prevalence of alternative foraging tactics in streams with lower spatial predictability in food resources likely produced strong effects on size frequency differences among treatments. As with other experimental analyses of salmonid behavior (e.g., Pucket and Dill 1984), floaters were less successful at acquiring food and were forced to invest more energy in agonistic activity as the result of being chased, and thus likely experienced reduced growth relative to territory holders. The higher proportion of individuals adopting floater foraging tactics may explain the increasingly negatively skewed size-frequency distributions and greater degree of size inequality that accompanied the decrease in the spatial predictability of food resources. While a pattern of increasing size inequality is often attributed to the intensity of competition (Begon 1984; Keeley 2001), our results provide experimental evidence for predictions that the form of intraspecific competition may also influence patterns of size frequency within populations (Łomnicki 1978).

In addition to effects on fish size frequencies, differences in the spatial predictability of food resources strongly influenced patterns of phenotypic selection within steelhead populations. Individuals with faster rates of energy metabolism were favored in streams with spatially predictable food resources, as evidenced by the selective retention of individuals having, on average, larger otoliths at emergence. The selective advantage of faster rates of energy metabolism during interference competition reflects a strong correlation between standard metabolic rate (SMR) and dominance in interference competition in salmonid fish, a result that has previously been shown both through direct measurements of SMR (e.g., Metcalfe et al. 1995;

Cutts et al. 2001; McCarthy 2001) and by using otolith size at emergence as a proxy for individual differences in SMR (Titus and Mosegaard 1991; Metcalfe et al. 1992; Yamamoto et al. 1998). While higher levels of SMR can be considered a potential energetic cost for an individual, increased rates of energy metabolism are linked to aggressive behaviors that improve resource acquisition (reviewed in Careua et al. 2008; Biro and Stamps 2010; and Burton et al. 2012). This fact may also help explain the moderate but significant positive correlation between otolith size at emergence and fish growth observed in spatially predictable streams, a result similar to a recent experimental analysis of juvenile Atlantic salmon (*Salmo salar*) (Hogenboom et al. 2012). Consequently, individuals with faster energy metabolism may have offset their increased energetic costs of maintenance by monopolizing food resources through territoriality, but apparently only in habitats where the distribution of food resources is spatially predictable.

In streams with the lowest spatial predictability of food resources, patterns of selection on energy metabolism were strikingly different. The selective advantage of faster energy metabolism should be reduced or neutralized when resources are less defendable and the energetic costs of possessing a high SMR cannot be offset through feeding territoriality (Hoogenboom et al. 2012). Consistent with this expectation, individuals with lower rates of energy metabolism were favored in streams with spatially unpredictable food distributions. Consequently, patterns of selection on energy metabolism paralleled our observations of reduced territoriality in highly unpredictable streams. These results are also consistent with previous studies showing that energy-efficient phenotypes (i.e., those with low maintenance costs) are favored in environments with low or fluctuating food availability (Bang and Grønkjær 2005; Artacho and Nespolo 2009).

Selection tended to be disruptive with respect to energy metabolism in streams with intermediate levels of spatial predictability in food resources. Visualization of selection surfaces using cubic splines suggested consistent patterns of disruptive selection on otolith size at emergence, although quadratic selection coefficients were statistically significant in parametric selection analyses in only two of the four streams. Disruptive selection indicates that extreme phenotypes were favored over individuals with intermediate values for energy metabolism. This pattern may have occurred if individuals with intermediate levels of energy metabolism had neither a sufficient level of aggression to acquire a feeding territory, nor low enough maintenance energy demands to balance the lower food intake rates of the floater foraging strategy. Taken together, the alternative modes of selection we observed indicate that variation in the spatial predictability of food resources during early ontogeny in *O. mykiss* may result in physiologically divergent populations.

Conclusions

Our results illustrate that individual and population responses to heterogeneous but spatially predictable food resources support several key predictions of IFD and IDD models (Fretwell 1972). In spatially predictable environments, individuals that can monopolize resources through territoriality were favored, and variation in patch quality altered territory size and local animal density. These compensatory adjustments resulted in more even partitioning of resources among individuals and tended to normalize components of fitness (e.g., growth) across heterogeneous environments. However, when the spatial predictability of resources declined to the point where resource defense became uneconomical for significant numbers of individuals, populations did not conform to IFD or IDD. Low spatial predictability of resources resulted in a greater total

abundance of animals, but a mismatch between patch-specific animal abundance and food quantity, greater discrepancy in the partitioning of food resources among individuals, and physiologically divergent populations. Our results indicate that the spatial predictability of food resources is an important determinant of individual and population characteristics. We suggest that spatial predictability of resources is an important but understudied component of habitat structure. Studies that manipulate the spatial predictability of resources may be especially promising for integrating dynamics of individual behavior, habitat selection, and population demography.

Acknowledgements

We thank Ryan Couture and staff at ODFW's Alsea River Hatchery for help obtaining fish for this experiment. Brian Nielsen and India Sloat helped with the construction of the experimental streams. Jerri Bartholomew, Don Stevens, and Jill Pridgeon provided access to the OSU's Salmon Disease Lab. Special thanks to Don Stevens for his assistance with fish rearing and experimental setup. Mike Reeves and Amy Lindsley extracted and polished hundreds of otoliths. Funding for this work was provided by the USDA Pacific Northwest Research Station and the Oregon American Fisheries Society Carl Bond Memorial Scholarship. The use of animals in this experiment was conducted under OSU Animal Care and Use Permits # 3923 and 4019.

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Chapter 4—Individual condition, behavior, and temperature influence life history expression in rainbow and steelhead trout (*Oncorhynchus mykiss*)

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Abstract

We reared behaviorally dominant and subordinate groups of juvenile *Oncorhychus mykiss* under alternative thermal regimes to determine the effects of these proximate influences on life-history expression in a partially migratory salmonid fish. Males and females exhibited large differences in the expression of anadromous and resident life histories, with males having higher overall rates of freshwater maturation. Behavioral dominance, determined through territorial contests for food and space, was associated with a decreased rate of freshwater maturation in females but not in males. Behaviorally dominant fish had significantly higher standard metabolic rates (SMR) than subordinate fish and may have had less residual energy for gonad development as a result of their higher costs of maintenance. Variation in individual growth in mass over time significantly influenced the probability of freshwater maturation, but produced paradoxical results: the fastest-growing individuals within each temperature treatment had the highest probability of freshwater maturation, but increases in rearing temperature had a negative effect on rates of freshwater maturation despite significantly improving somatic growth rates. Differences in whole-body lipid content in fish reared under the two temperature regimes may resolve this paradox. Fish reared at cold temperatures had significantly higher whole-body lipid content than those reared at warm temperatures. Freshwater maturing females also had significantly higher whole-body lipid content than anadromous females, after controlling for the effects of temperature. These results indicate that a combination of body size and energy content are important predictors of salmonid life histories. Our study highlights some of the challenges of predicting the life-history responses of phenotypically plastic species to alterations in stream temperature.

Introduction

In many populations, individual animals express a range of migratory behavior (Dingle 1996). For some individuals, ontogenetic niche shifts involve migrations of thousands of kilometers, while others remain sedentary by comparison, completing their entire life cycle within a narrow home range. Such a diversity of migratory behavior is termed partial migration (Chapman et al. 2011), and is exhibited by many species of salmonid fish (Jonsson and Jonsson 1993; Dodson et al. 2013). Partially migratory salmonid populations consist of anadromous individuals that undergo marine migrations before reaching maturity, and freshwater residents that complete their entire life cycle in freshwater streams. The two forms commonly interbreed and the offspring of one from can give rise to the other (e.g., Seamons et al. 2004; McPhee et al. 2007; Christie et al. 2011).

The expression of alternative migratory phenotypes—whether an individual becomes anadromous or remains a freshwater resident—can be shaped by a variety of proximate influences. Previous research has demonstrated that factors influencing energy budgets and growth during freshwater rearing are especially important for the expression of alternative migratory phenotypes (e.g., Thorpe et al 1998; Forseth et al. 1999; Morineville and Rasmussen 2003). Individual variation in energy metabolism and environmental temperature are two factors that may exert strong influences on patterns of energy allocation and life histories that have received relatively little attention to date. In salmonid fish, standard metabolic rate (SMR) varies several-fold among individuals even after accounting for variation in body mass (Enders and Scruton 2005; Tyler and Buldoc 2008). A consequence of this variation is that individuals may exhibit divergent responses to environmental factors influencing food acquisition and conversion

efficiency (Van Leeuwen et al. 2011). For a given food intake, an individual with elevated maintenance costs imposed by higher SMR may have significantly less surplus energy available for growth and competing functions such as maturation (Van Leeuwen et al. 2011; Reid et al. 2012). Because energy budgets exert a strong influence on life-history decisions, variation in energy metabolism is likely to be an important proximate influence on life histories.

Temperature exerts a similar influence on individual maintenance costs through its direct effects on metabolism in teleost fish (Clarke and Johnston 1999). Assuming equal food intake, increases in temperature elevate the energy needed for maintenance and, thus, may reduce energy available for competing functions. Because of the anticipated effects of stream warming from global climate change (van Vliet et al. 2010; Isaak et al. 2011), understanding the proximate influence of temperature on life-history decisions is critical for the conservation of salmonids. Unfortunately, predicting the effects of temperature on ectotherm life histories is challenging (e.g., Bernardo and Reagan-Wallin 2002). Recent models used to predict the influence of elevated temperatures on salmonid life histories (e.g., Satterthwaite et al. 2010; Benjamin et al. 2013) assume simple linkages between stream temperature, somatic growth, and life-history expression. In these models, favorable increases in temperature are predicted to result in improved somatic growth, which is assumed to trigger increased rates of freshwater maturation within a population. However, recent field research has demonstrated that stream temperature can influence fish bioenergetics in more complex ways than simply affecting somatic growth. Food consumed by fish can be allocated to alternative energetic pathways, including energy used either for growth or for storage in the form of lipid reserves. McMillan et al. (2012) found that stream temperature influenced relative energy allocation to growth and

storage in *O. mykiss* populations in the John Day River basin, Oregon, USA: in warm streams, fish exhibited higher somatic growth but allocated less energy into storage as lipid reserves as compared to fish in cold streams. A reduction in energy storage with increasing stream temperature has consequences for life-history expression because lipid content is positively correlated with freshwater maturation in salmonids (e.g., Simpson 1992; Silverstein et al. 1997; McMillan et al. 2012). Thus, increasing stream temperatures may not necessarily result in increased freshwater maturation in *O. mykiss*, even if elevated temperatures increase somatic growth rates. Given the complex responses of ectotherms to changes in temperature, a mechanistic understanding of physiological responses to altered thermal regimes is needed to forecast effects of climate change.

In this study, we conducted an experiment to determine the influence of temperature, fish behavioral type, and individual condition on the expression of anadromy or freshwater maturation in partially migratory steelhead and rainbow trout (*Oncorhynchus mykiss*). To examine the effect of fish behavior, and potentially correlated physiological traits, we separated fish into socially dominant and subordinate groups through behavioral assays conducted in laboratory stream channels. We then reared these groups in a series of replicated tanks subjected to two alternative thermal regimes until they exhibited the outward expression of traits associated with anadromous and maturing phenotypes. By tracking individual body size throughout the experiment, we examined how temperature, behavioral phenotypes, and individual growth trajectories influenced life-history expression.

Materials and methods

Synopsis of life history

Partially migratory populations of *O. mykiss* consist of interbreeding anadromous and freshwater-maturing forms (Seamons et al. 2004; McPhee et al. 2007; Christie et al. 2011). Both forms spawn in streams in late-winter through spring, and the young live as parr in freshwater for one or more years before they either smolt and migrate to sea in the spring or mature and complete their life cycle entirely within freshwater. The process of smolting involves behavioral and physiological preparations for the transition from life in freshwater streams to life in the marine environment. Resident fish may attain maturity as early as one year after hatching, but typically require two or more years of rearing before maturity. Anadromous fish attain maturity after an additional one to four years in the sea before returning to freshwater for spawning.

Collection and rearing of experimental animals

We used a full-sibling group of juvenile *O. mykiss* from the Clackamas River, Oregon, USA for the experiment. Fish were obtained as fertilized eggs from Oregon Department of Fish and Wildlife's Clackamas River Hatchery. We used a group of fullsiblings produced from mating a single anadromous adult male and female captured at the Clackamas River Hatchery. Immediately after fertilization, eyed eggs were transferred to Oregon State University's Salmon Disease Laboratory, Corvallis. Fish were incubated at 10°C until completion of yolk-sack absorption and the onset of exogenous feeding, at which point they were selected for inclusion in the experimental trials.

Determination of fish dominance status

Prior to conducting the growth experiment, we separated fish into subordinate and dominant behavioral groups based on competitive outcomes in laboratory streams. To determine dominance status of fish, we stocked a series of 12 laboratory streams at densities of 100 fish·m^{-2}

and allowed fish to either establish and defend feeding territories within the streams or emigrate into a one-way fish trap at the downstream end of the channel (Keeley 2001). The goal of this procedure was to use fish behavior to separate a full-sibling cohort into two groups that differ in their competitive ability. Because of a positive correlation between metabolic rate and competitive dominance (e.g., Metcalfe 1995; Yamamoto et al. 1998; McCarty 2001), we hypothesized that fish successfully establishing and defending territories within the experimental streams would, on average, have higher standard metabolic rates than emigrating fish. We assumed that emigrating fish were competitively excluded from the stream channels, an assumption well supported by the literature (e.g., Chapman 1962; Titus and Mosegarrd 1991; Elliot 1990).

The laboratory streams consisted of 2.4 m x 0.5 m rectangular channels with gravel substrate and a one-way fish emigration trap at the outflow. Water depth was a uniform 15 cm. Flow rate through the channels was approximately 2 $m^3 \cdot hr^{-1}$. Three 14 x 5 x 8 cm bricks were evenly spaced down the center of each stream to provide physical structure for fish orientation. We provided food to the experimental streams via automated belt feeders that dispensed 1.44 grams of Biodiet starter feed (Bioproducts, Warrenton, Oregon, USA) to the head of the channel over a 12-hr period beginning at 07:00 each day. Directional flow within the streams distributed food throughout the channel. We removed emigrants from the trap daily and held them in a single 100-L tank. We allowed emigration to proceed until there were approximately 35 fish in each channel, a period of 4 or 5 days, at which point the remaining fish were removed from the channels and held in a separate 100-L tank. Based on behavioral observations in this and previous studies that we conducted within the stream channels, we assumed that emigrant fish

were competitively excluded from the stream channels and that the last 35 fish retained within the streams were competitively dominant (hereafter, we refer to these fish as “territorial” fish). Previous experiments using this methodology demonstrated that otolith size at emergence was, on average, larger in fish retained within the streams than in emigrants (Chapter 2), indicating that fish retained within the experimental streams had faster rates of energy metabolism (Wright 1991; Titus and Mosegaard 1991; Yamamoto et al. 1998). Consequently, we expected fish that had remained within the streams and those that emigrated to represent two divergent behavioral and physiological groups that could differ in their propensity for anadromous or freshwater-maturing life histories.

Dominance trials between territorial fish and stream emigrants

To test the assumption that stream emigrants were competitively excluded from the experimental stream channels, we determined the competitive outcomes of contests between a subsample of territorial fish and emigrant fish in dyad trials. Territorial fish and emigrants from experimental stream trials were size-matched and paired in 25 dyads. Fish from each dyad were then individually marked using colored visible implant elastomer (VIE) injected within dorsal fin tissue before being placed in a simulated stream environment consisting of 0.45 m-long x 0.15 m-wide x 0.15 m-deep channels. The channels had directional flow and a natural substrate of gravel. Food was provided by introducing frozen brine shrimp through a feeding tube located at the head of each channel. Fish were allowed 24 hours to acclimate to the channels, and then were observed during controlled feeding to determine differences in the direction of agonistic interaction and rate of food acquisition between individuals.

Respirometry

Respiration of behaviorally dominant and subordinate fish (i.e., fish that remained in the experimental streams and stream emigrants, respectively) was measured using intermittent-flow respirometry by placing individual fish into four separate glass chambers, allowing measurement of SMR on four fish per day. Two respirometry chambers each were submerged in two 100-L tanks supplied with a constant inflow of oxygenated water at 13°C. Water was supplied to each respirometry chamber via two submersible centrifugal pumps. A flush pump supplied oxygenated water from the 100-L water bath. A second pump recirculated water through the respirometry chamber in a closed loop. Oxygen concentration was measured using a fiber optic oxygen sensor and oxygen meter (Oxy-4 mini oxygen instrument, Loligo Systems, Tjele, Denmark) sealed within a flow-through cell in line with the recirculating pump. To measure oxygen consumption, the flush pump was intermittently turned off, during which time the depletion of oxygen in the respirometry chamber was measured, and then turned back on to restore the oxygen content of the respirometry chamber back to pre-measurement levels. Measurement of oxygen consumption was made at approximately 7-min intervals during a 16-h period from 16:00 on the day each trial began to 8:00 on the following day. Control of the pumps and calculation of oxygen consumption rates for each measurement period were automated using AutoResp™ software (Loligo Systems).

Due to logistical constraints, we could not conduct respirometry trials until 9 months after the behavioral assessments were performed. Previous research has shown that relative rates of energy metabolism in laboratory-reared salmonines are stable over periods of 6 – 9 months (McCarthy 2000; Cutts et al. 2001), suggesting that our SMR measurements are still likely to

capture the relative metabolic performance of individuals even if they do not reflect rates of energy metabolism at the time that dominance status was assessed. Prior to being placed in respirometry chambers, all fish were held without food for 30 hours prior to ensure gut clearance and that fish were in a post-digestive state during SMR measurement. We measured fish mass to the nearest 0.01 g using an electronic balance, and fish volume to the nearest mL using water displacement in a graduated cylinder immediately before placing fish in the respirometry chambers. Measuring these parameters facilitated the automated calculation of oxygen consumption rates. Oxygen consumption rates were plotted graphically, and SMR was estimated as the median of the lowest six measurements, which always occurred > 9 hours after the fish were introduced to the chambers.

Experimental rearing

We used a two-by-two factorial design to test the effects of temperature and dominance status on growth and development in juvenile *O. mykiss*. We reared a total of 24 groups of 30 fish in a series of 100-L tanks. These groups consisted of 12 groups of behaviorally dominant fish and 12 groups of behaviorally subordinate fish, as determined using the laboratory streams described above. Six groups of fish from each behavior type were subjected to one of two thermal regimes that differed by an average of 2.5°C mean annual water temperature. A warm regime consisted of seasonally adjusted temperatures between 6 – 18°C and the cool regime ranged between 6 - 13°C (Figure 4.1). The two thermal regimes were achieved using in-line heater and chiller units that adjusted water from an ambient temperature of 13°C. Water temperatures were recorded at 1-hr intervals using water temperature data loggers (HOBO Pro v2, Onset Corp., Pocasset, MA, USA). Fish were reared under a natural photoperiod (45°N).

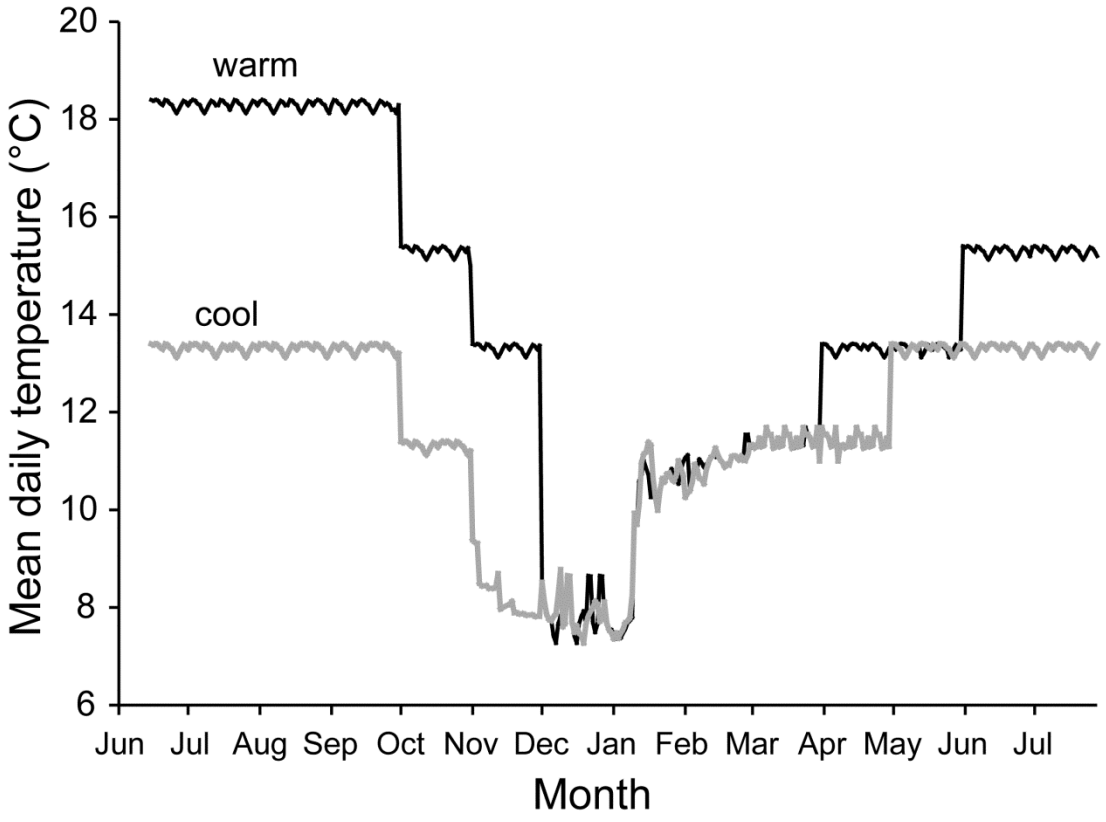

Figure 4.1. Water temperatures in warm and cold experimental thermal regimes from June 2010 to July 2011.

Mortality rates over the 13 month-long growth trials ranged from 1 to 6 individuals per tank, with no difference in mortality between treatment groups (ANOVA, effect of temperature, $F_{1, 22} = 3.814$, $P = 0.190$; effect of behavior, $F_{2, 22} = 0.4847$, $P = 0.623$). We maintained constant fish densities within each tank by replacing any mortalities with fish of a similar behavioral type reared under the appropriate thermal regime. Data from replacement fish were not analyzed. A logistical failure resulted in excessive fish mortality (> 50%) in one tank within the cold temperature, dominant fish treatment. Data from this tank were not included in any analyses.

Fish were hand-fed pellet feed (Bioproducts, Warrenton, Oregon, USA) twice daily at a ration size of 3% mean body mass per day, adjusted monthly for fish growth. We tracked the size of individual fish using unique color and location combinations of VIE marks. At monthly intervals from June 2010 – July 2011, we anaesthetized all fish and measured fork length (FL) to the nearest mm, and mass to the nearest 0.01 g.

Determination of life histories

We determined the life histories of individual fish using a combination of visual examination and dissection. During May and June 2011, the period when smolts from the source population normally migrate to sea, we visually assessed each fish to determine whether their phenotypic characteristics were consistent with smoltification. During this period, migratory phenotypes become silver in color, lose parr marks and fin coloration, and their morphology becomes more fusiform (Jonsson 1985; Tanguy et al. 1994; Nielsen et al. 2003). At the conclusion of the experiment, we euthanized all fish and dissected their gonads to determine the sex and maturation stage. Fish were categorized as mature, maturing, or non-maturing depending on the stage of gonad development. Maturation status in males was determined by visual examination of testes. Maturing fish had moderately enlarged, white testis, visible without microscopy, but without running milt (Jones and Orton 1940; McMillan et al. 2011). Fully mature males had enlarged white testis and running milt. Non-maturing males had gonads visible only with the aid of microscopy and aceto-carmine stain (Guerrero and Shelton 1974). Maturation status in females was determined by histology. Ovaries were removed and fixed in formalin and then dehydrated through a graded series of ethanol baths and embedded in paraffin wax, sectioned (thickness, 5 µm), and stained with hematoxylin-eosin to aid in visualization of

oocytes. Development stage (oogenesis) was determined by light microscopy (Nagahama 1983). No females were fully mature at the end of the growth trials, but females were classified as maturing in preparation for reproduction in the subsequent spring if oocytes had advanced to lipid droplet stage at the time of sampling (Nagahama 1983; Campbell et al. 2006). Males and females that exhibited neither the phenotypic characteristics of smolting nor maturing gonads were considered to have undetermined life histories at the time of sampling. At the conclusion of the study, whole-body lipid content was determined in a random selection of 30 males and 30 females per life-history type per temperature treatment. Whole-body lipid content (to the nearest 0.01%) was determined using the acid hydrolysis method (Anonymous 1987; AOAC 1998).

Data analysis

Data for males and females were treated separately in all analyses. To test for treatment effects on the proportion of fish maturing during the experiment, we performed analysis of variance (ANOVA) on arcsine-square root transformed data. To determine treatment effects on mass-at-age trajectories, we performed repeated measures analysis of variance (ANOVAR) on replicate tank mean values. We also analyzed patterns of fish growth to determine if the influence of treatments on life-history expression was expressed primarily through effects on individual fish growth. Individual mass-at-age trajectories under the conditions of our study were well described by a Gompertz growth equation (Winsor 1932), a model of asymptotic growth that is commonly used to describe the growth form of fish (Quinn and Deriso 1999):

$$m_t = m_\infty \mathrm{e}^{-\mathrm{e}^{-k(t-I)}},$$

where m is mass, m_∞ is the asymptotic size, k is growth rate, t is age, and I is the age at the inflection point (Figure 4.2). The model was fitted to the monthly individual mass measurements using non-linear least-squares regression.

We also investigated potential seasonal growth effects on life-history expression by calculating absolute growth in mass ($g \cdot day^{-1}$) for each fish during the summer/fall (July – November), winter (November – March), and spring (March – June) periods. We then performed logistic regression using these growth parameters and treatment levels to estimate the probability that an individual fish would either mature or smolt. The full statistical model for this analysis was:

$$\text{logit}\,[p(m)] = \beta_0 + \beta_1(T) + \beta_2(B) + \beta_3(m_\infty) + \beta_4(k) + \beta_5(I) + \beta_6(g_s) + \beta_7(g_w) + \beta_8(g_{\text{spr}}) + \beta_9(m_f) + \alpha + \varepsilon,$$

where T is temperature regime, B is behavioral group, m_∞, k, and I are Gompertz growth curve parameters, as previously described, g_s, g_w, and g_{spr} are summer, winter, and spring absolute growth rates, respectively, m_f is mass at the end of the growth trials, α represents a random tank effect, and ε is a random error term. The analysis was run separately for males and females. These mixed effect models where fitted using the lmer procedure in the lme4 library (Bates 2013) in R 2.12.1 (R Development Core Team 2010). We used Akaike's information criterion (AIC) to select the most parsimonious model from the set of candidate models, given the data (Burnham and Anderson 2002). The model with the smallest AIC value was regarded as the most plausible, given the data, and models within two AIC units of the model with the lowest AIC value were considered to be equally supported by the data.

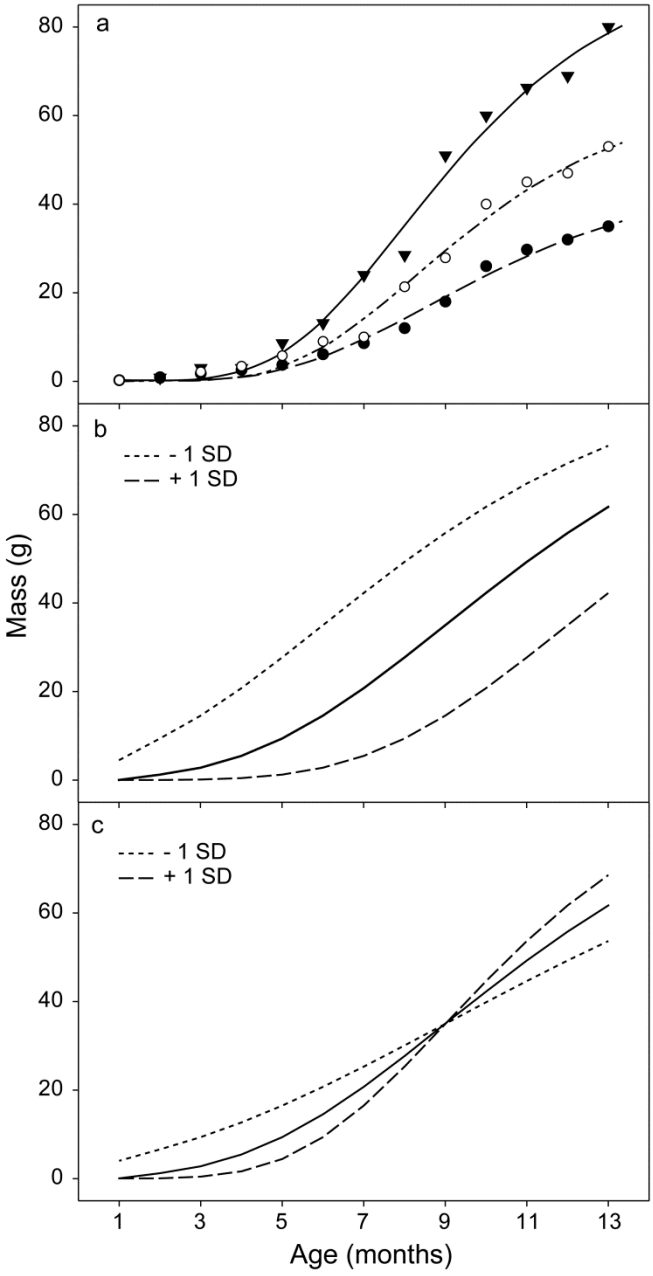

Figure 4.2. (a) Three examples of the Gompertz growth equation fit to individual mass-at-age data for three *O. mykiss*. Age is expressed as months after hatching. (b) An illustration of variation in the inflection point (*I*). For a fixed m_∞ and *k*, growth curves are plotted for the mean *I* (solid line) and one standard deviation above (dashed line line) and one standard deviation below (dotted line) the mean. (c) An illustration of variation in growth rate (*k*). For a fixed asymptotic size (m_∞) and inflection point (*I*), growth curves are plotted for the mean *k* (solid line) and values one standard deviation above (dashed line) and one standard deviation below (dotted line) the mean.

Results

Individual behavior and energy metabolism

Dyad trials

Dyad trials confirmed the patterns of dominance inferred from the behavior of fish within larger social groups in experimental stream channels. When placed in dyads with previous stream emigrants, fish that had previously remained within the experimental streams consumed 78% of the introduced food items (χ^2 = 24.106, d.f. = 1, $P < 0.001$), initiated 79% of agonistic encounters (χ^2 = 6.368, d.f. = 1, $P = 0.012$), and were considered dominant in 20 of 25 trials (80%). Consequently, individuals that we inferred as being dominant within the experimental stream channels were 16 times more likely to be dominant when paired in dyads with previous stream emigrants (χ^2 = 15.680, d.f. = 1, $P < 0.001$).

Standard metabolic rate (SMR)

Dominant fish had significantly higher SMR than subordinate fish (i.e., experimental stream emigrants) (Figure 4.3). Behaviorally dominant fish shared a common slope with subordinate fish in regressions of log(mg $O_2 \cdot h^{-1}$) on log(mass) ($F_{1,38}$ = 0.02, P = 0.881), but had a significantly higher intercept ($F_{1,38}$ = 9.830, P = 0.008). Consequently, for a given body mass dominant fish had, on average, a 1.0 mg $O_2 \cdot h^{-1}$ higher SMR relative to subordinate fish over the range of fish size that we sampled (Figure 4.3).

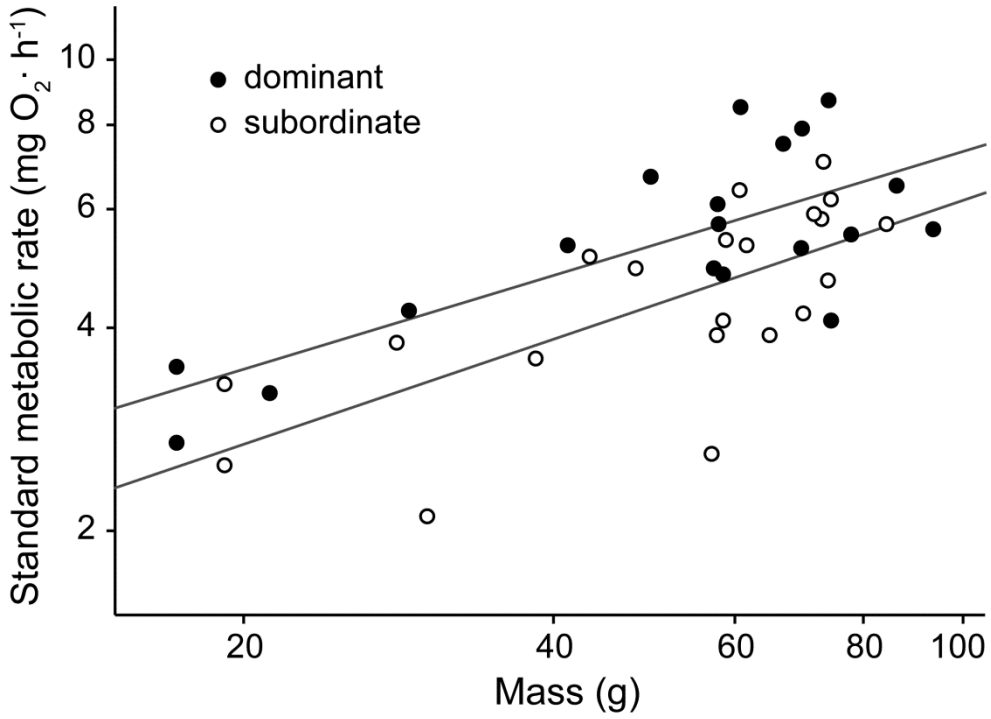

Figure 4.3. The relationship between standard metabolic rate and mass for behaviorally dominant and subordinate juvenile *O. mykiss.*

Growth trials

Treatment effects on maturation

There was no difference in the proportion of males and females within any of the treatment groups (χ^2 = 2.542, d.f. = 3, P = 0.468). On average, among the four combinations of behavioral type and rearing temperature, 22% to 42% of females initiated maturation during the experiment (Figure 4.4). No females were capable of reproduction by the end of the experiment, but maturing females had reached the lipid droplet stage of oocyte development (Nagahama 1983; Campbell et al. 2006) in preparation for reproduction the following spring. Temperature had a significant negative effect on the proportion of females maturing (ANOVA on arcsine

square root-transformed data, $F_{1, 19} = 22.810$, $P < 0.001$). The mean proportion of females maturing under the cool thermal regime was 18% greater (95% Confidence Interval [C.I.] = 9 – 28%) than in the warm regime. Behavioral type had a weak but significant effect on female rates of maturation (ANOVA, $F_{1, 19} = 5.107$, $P = 0.036$). Groups of behaviorally dominant females had a 9% (95% C.I. = 1 – 17%) lower mean rate of maturation, after allowing for the effects of temperature on life-history expression. We could not determine the life-history phenotype of 6% of females, with neither temperature nor behavioral type having an effect on the proportion of undifferentiated females (ANOVA, effect of temperature, $F_{1, 19} = 0.001$, $P = 0.973$; effect of behavior, $F_{1, 19} = 2.808$, $P = 0.110$).

Overall, the mean rate of male maturation during the experiment was 30% higher (C.I. = 21 – 40%) than in females. Among the four combinations of behavioral type and rearing temperature, 47% to 82% of males initiated maturation (Figure 4.4). Temperature had similar effects on life-history expression in males as in females: males exposed to the cold thermal regime had a 26% (95% C.I. = 16 – 35%) higher rate of maturation (ANOVA on arcsine square root-transformed data, $F_{1, 19} = 19.398$, $P < 0.001$) than those exposed to a warm thermal regime. Behavioral type did not influence life-history expression in males (ANOVA, $F_{1, 19} = 0.394$, $P = 0.538$). Although overall male maturity rates were lower in warmer temperatures, the proportion of maturing males that were fully mature at the end of the experiment was 56% (95% C.I. = 41 – 69%) higher in the warm temperature treatment (ANOVA, $F_{1, 19} = 61.961$, $P < 0.001$). We could not determine the life-history phenotype of 6% of males, with neither temperature nor behavioral type having an effect on the proportion of undifferentiated males (ANOVA, effect of temperature, $F_{1, 19} = 0.298$, $P = 0.591$; effect of behavior, $F_{1, 19} = 1.127$, $P = 0.302$).

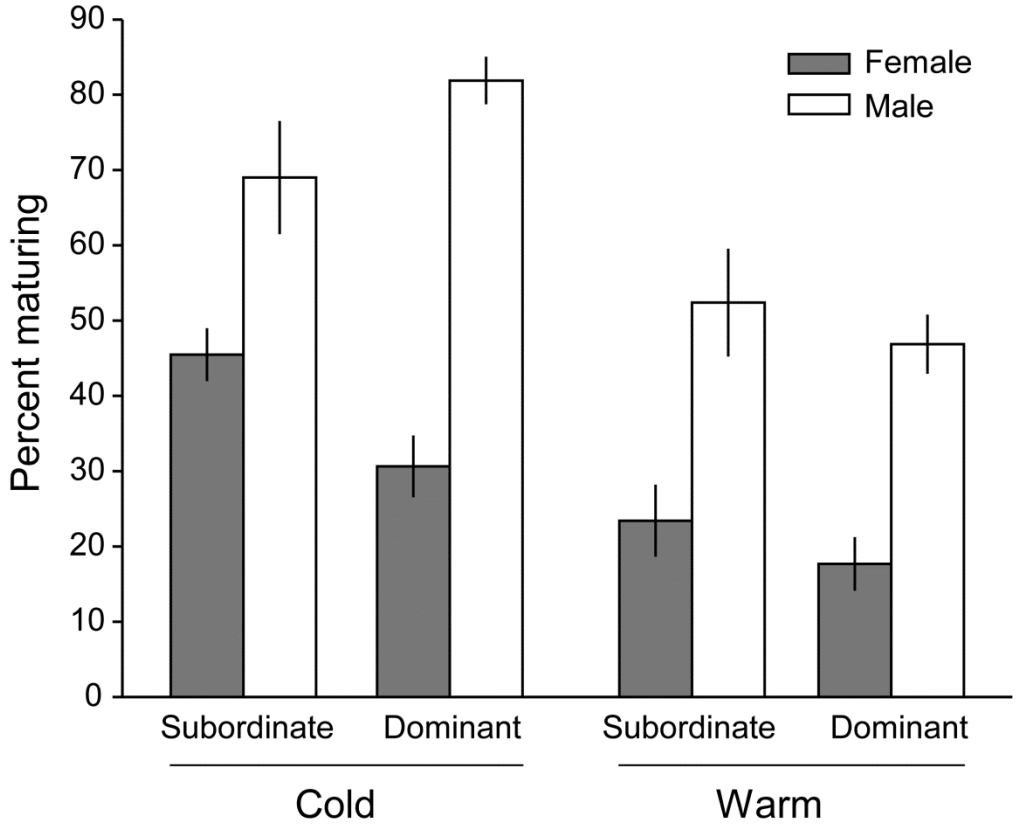

Figure 4.4. Mean rates of maturation (%) for male and female *O. mykiss* by behavior type and temperature treatment. Error bars represent ± 1 SE.

Effect of growth form on *O. mykiss* life histories

For both males and females, temperature had a significant effect on the change in mass over time (ANOVAR, effect of temperature in females, $F_{1, 231} = 89.758$, $P < 0.001$; effect of temperature on males, $F_{1, 231} = 53.808$, $P < 0.001$). Growth trajectories among temperature treatments began to diverge in November (Figure 4.5), giving rise to a significant temperature × date interaction (ANOVAR, temperature × date interaction in females, $F_{1, 12} = 1249.542$, $P < 0.001$; temperature × date interaction in males, $F_{1, 231} = 42.610$, $P < 0.001$). In both males and

females, there was a consistent pattern for groups of subordinate fish to have a lower mean mass at age than dominant groups (Figure 4.5). However, the magnitude of the difference between behavioral types never reached statistical significance for either males or females in either temperature treatment (ANOVAR, effect of behavior in females, $F_{1, 12} = 0.0224$, $P = 0.882$; effect of behavior in males, $F_{1, 231} = 0.0638$, $P = 0.803$).

In general, the Gompertz growth model fit individual growth trajectories very well, with R^2 values between 0.94 and 0.99. For some fish (4%), estimates of the asymptotic size parameter were highly uncertain (i.e., $P > 0.10$) and these individuals were removed from subsequent analyses of growth form and life-history expression. For the remainder of fish, this procedure provided individual estimates of the growth rate parameters $m_{\infty,}$ k, and I (Table 4.1). The best approximating logistic regression model of life-history expression in female *O. mykiss* included significant effects of the Gompertz growth model parameters m_{∞} and I, as well as effects of temperature treatment, and fish behavioral group (Table 4.2). Female maturation was positively associated with m_{∞} and negatively associated with I (Table 4.2) indicating that, on average, females with higher estimated asymptotic size and an earlier occurrence of inflection in the estimated growth curve had a higher probability of maturation (Figure 4.6). Interpretation of the effect of variation in I on individual growth trajectories is aided by Figure 4.2. For a given asymptotic size and growth rate, fish with lower values of I have relatively higher mass earlier in life. Consequently, the negative effect of I on the probability of female maturation suggests that females that were relatively larger at younger ages had a higher probability of maturation.

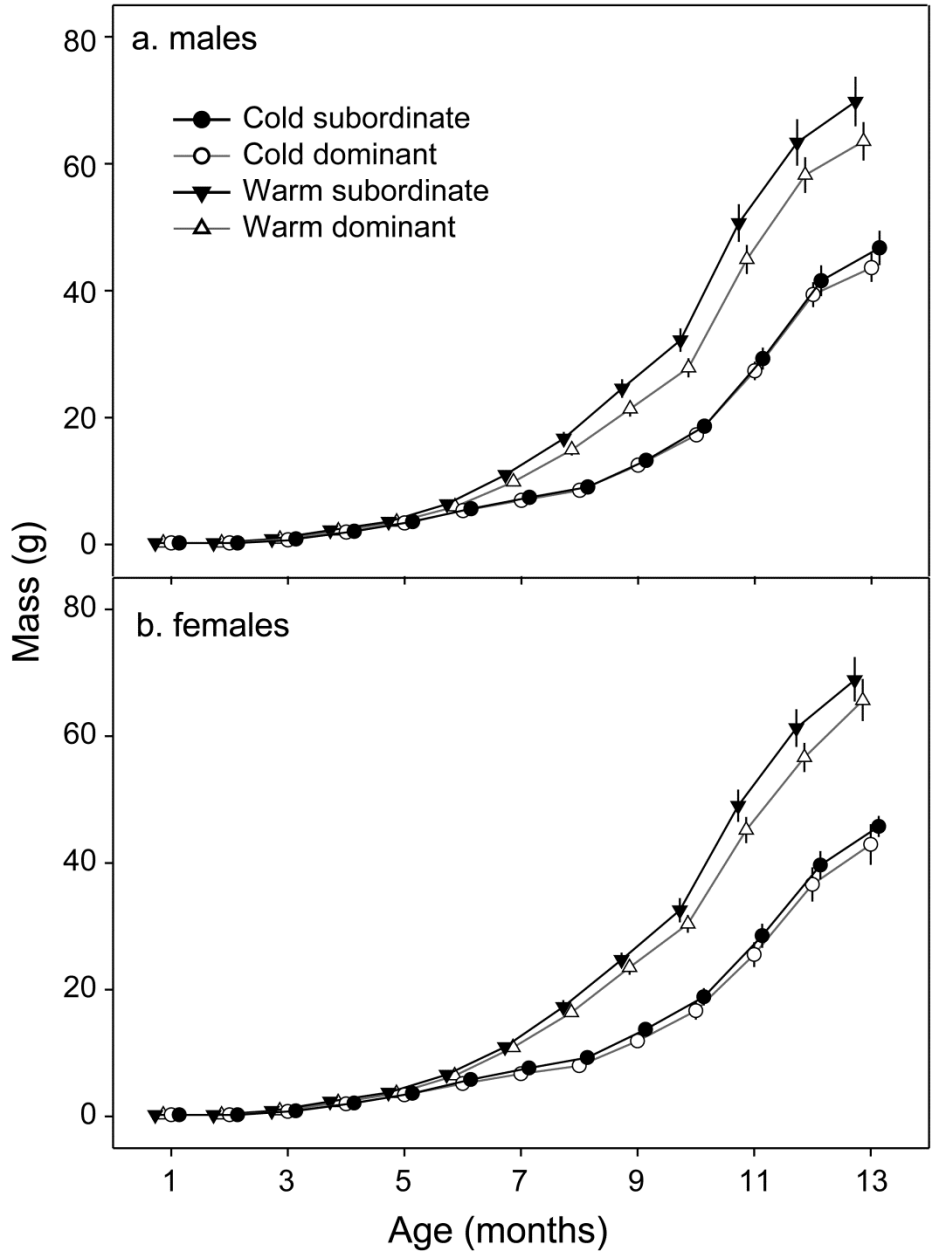

Figure 4.5. Mean mass-at-age for (a) male and (b) female *O. mykiss* over the 12-month period from June 2010 – July 2011. Data are organized by behavior and temperature treatment. Error bars represent ± 1 SE.

Table 4.1. Summary of growth parameters asymptotic size (m_∞), growth rate (k), and growth inflection (I) from a Gompertz growth equation fit to individual trajectories in mass-at-age in male and female *O. mykiss* expressing maturing or smolting phenotypes when reared under cold and warm thermal regimes.

Temperature and life history category	m_∞	k	I
	mean ± se	mean ± se	mean ± se
Females			
Cold			
Smolt	142.27 ±10.51	0.179 ±0.007	10.05±0.35
Mature	225.72 ±19.92	0.166 ±0.007	11.29±0.38
Warm			
Smolt	151.12 ±6.74	0.213 ±0.006	9.39±0.26
Mature	234.56 ±25.46	0.216 ±0.011	9.15±0.32
Males			
Cold			
Smolt	143.82 ±26.77	0.061 ±0.014	9.20±0.23
Mature	182.46 ±14.43	0.077 ±0.009	9.46±0.39
Warm			
Smolt	155.12 ± 8.09	0.064 ±0.007	10.87±0.59
Mature	182.12 ±12.00	0.085 ±0.009	11.45±0.33

Table 4.2. Best approximating mixed-effects logistic regression models of the probability of maturation in juvenile female and male *O. mykiss*, respectively. Variables retained in the best approximating models include temperature (*T*), behavioral group (*B*), and the Gompertz growth parameters asymptotic mass (m_∞), age at the inflection point (*I*), and growth rate (*k*) parameters estimated for individual fish. Model selection was based on minimum AIC values. Tank replicate was included as a random effect in all models.

Variable	Coefficient±SE	z-value	*P*
Female			
Intercept	1.530 ±0.935	1.636	0.102
T	-1.920 ±0.374	- 5.132	<0.001
B	-0.651 ±0.307	- 2.122	0.034
m_∞	0.013 ±0.002	5.152	<0.001
I	-0.277 ±0.088	- 3.170	0.002
Male			
Intercept	-0.148 ± 0.627	- 0.236	0.814
T	-1.793 ± 0.333	- 5.378	<0.001
m_∞	0.005 ± 0.002	2.872	0.004
k	4.909 ± 2.184	2.248	0.025

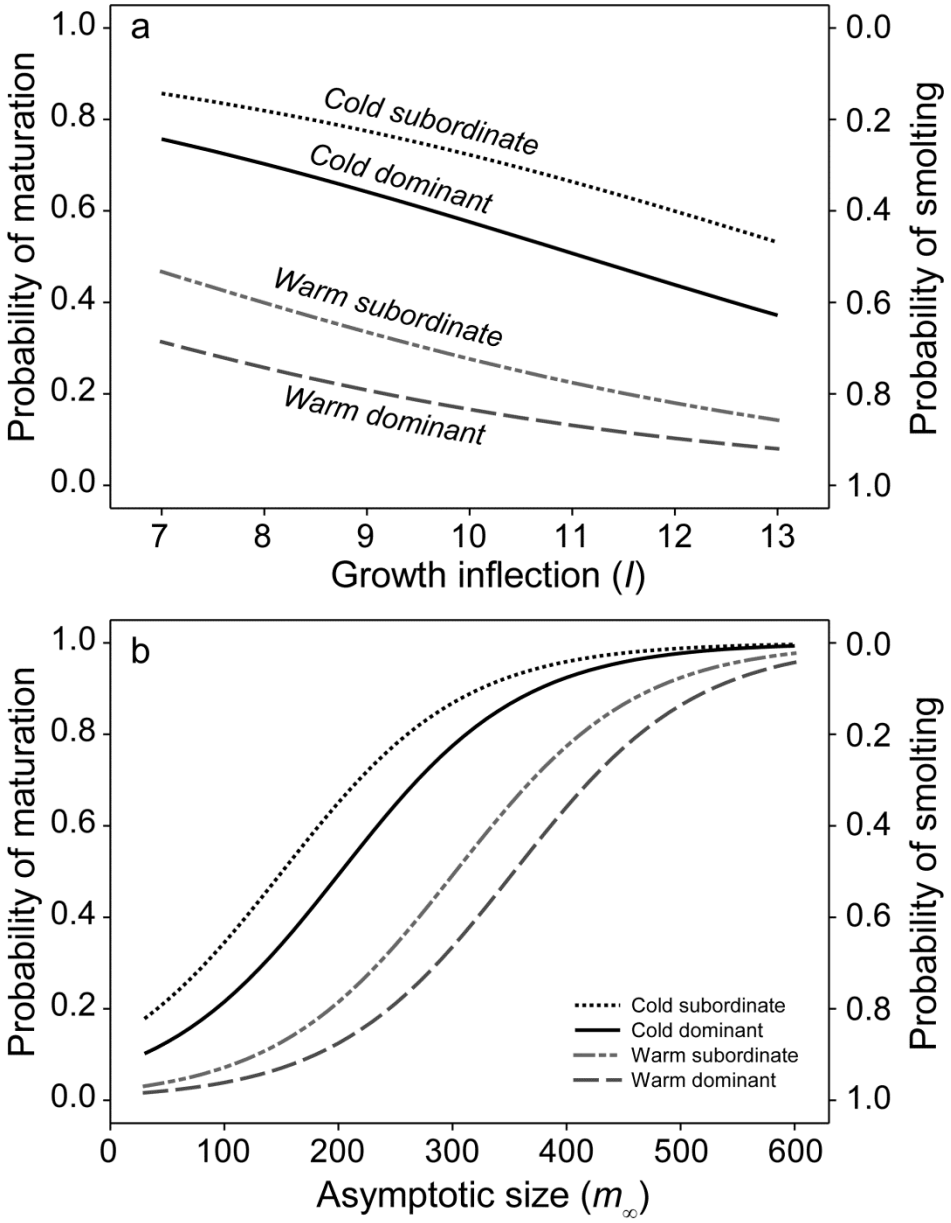

Figure 4.6. Predicted probability of life-history expression in behaviorally dominant and subordinate juvenile female *O. mykiss* reared under cold and warm thermal regimes as a function of variation in (a) growth inflection *(I)* and (b) asymptotic size (m_{∞}). Probability curves for *I* and m_{∞}, respectively, were estimated by using mean values for other growth parameters included in the best approximating multiple logistic regression model of female life-history expression (Table 4.2). In this analysis, probability of maturation (left *y* axis) is the reciprocal of the probability of smolting (right *y* axis).

The Gompertz growth rate parameter (*k*) was also positively associated with the probability of female maturation when included in a model with temperature, fish behavioral group, and asymptotic size ($z = 2.697$, $P = 0.007$) but did not warrant inclusion in the best approximating logistic regression model ($\Delta AIC = 3.4$). In addition to growth parameters, rearing temperature and behavioral dominance had negative effects on the probability of female maturation (Table 4.2). Since the logistic regression analysis only included those females expressing either maturing or smolting phenotypes, the probability of maturation represents the reciprocal of the probability of smolting (Figure 4.6). Thus, the reaction norms illustrated in Figure 4.6 represent probabilistic thresholds for the adoption of either freshwater-maturing or anadromous phenotypes in female *O. mykiss* under the conditions of our study.

For male *O. mykiss*, the best approximating logistic regression model of life-history expression included significant effects of the Gompertz growth model parameters m_∞ and *k*, as well as effects of temperature treatment (Table 4.2). Male maturation was positively associated with m_∞ and *k* (Table 4.2) indicating that, on average, males with higher estimated asymptotic size and higher growth rate had a higher probability of maturation (Figure 4.7). Temperature had a negative effect on the probability of male maturation (Table 4.2). As with the analysis of females, the logistic regression analysis only considered those males expressing either maturing or smolting phenotypes, so that the reaction norms illustrated in Figure 4.7 represent probabilistic thresholds for the adoption of either freshwater maturation or anadromy in male *O. mykiss* under the conditions of our study.

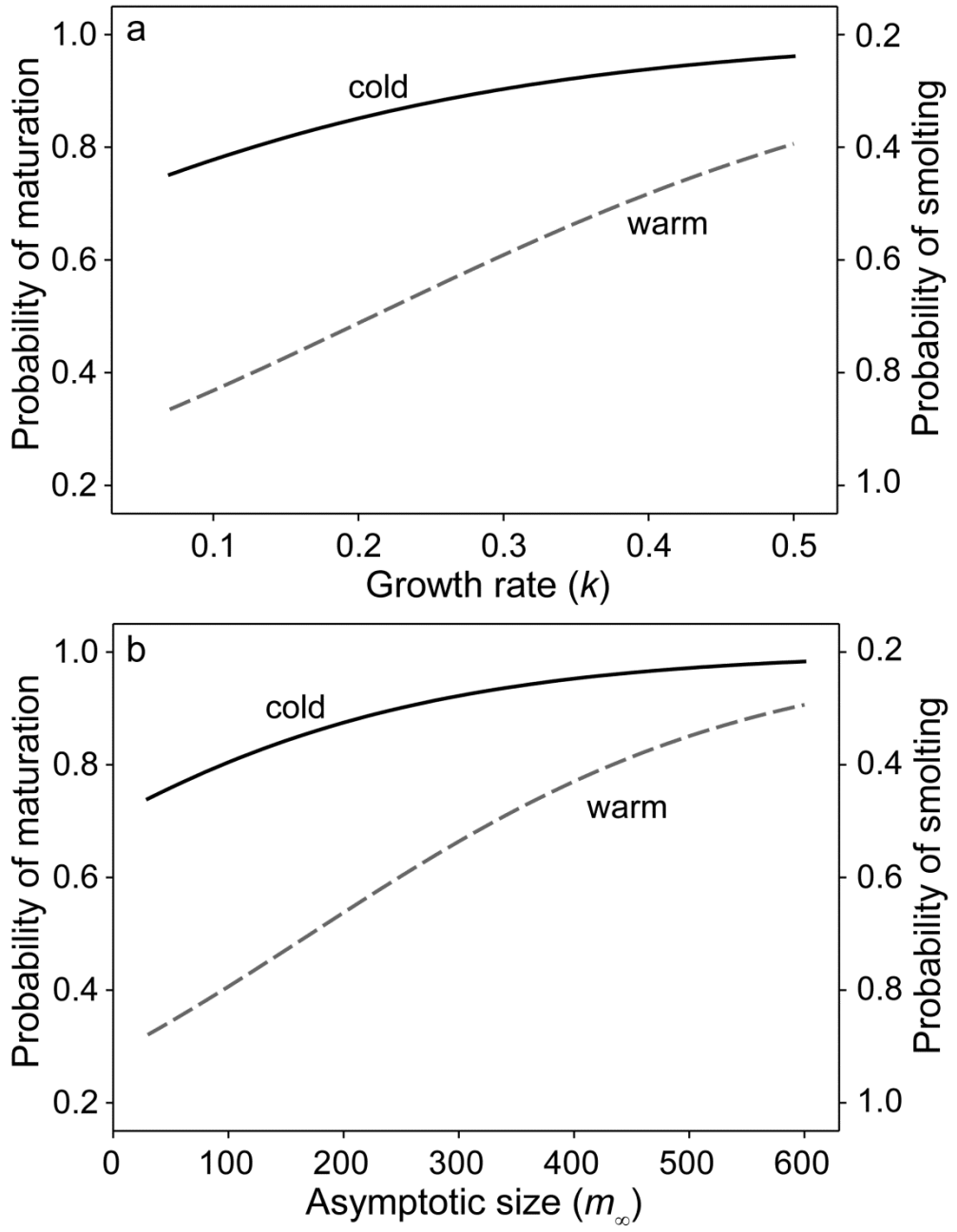

Figure 4.7. Predicted probability of life-history expression in juvenile male *O. mykiss* reared under cold and warm thermal regimes as a function of variation in (a) growth rate (k) and (b) asymptotic size (m_∞). Probability curves for k and m_∞ were estimated by using mean values for other growth parameters included in the best approximating multiple logistic regression model of male life-history expression (Table 4.2). In this analysis, probability of maturation (left y axis) is the reciprocal of the probability of smolting (right y axis).

Whole-body lipids

Mean whole-body lipid content for females was 9.2% (± 0.28 SE). When pooled across tank replicates, there were small but significant differences in whole-body lipid content between life-history types and temperature regimes (ANOVA, effect of temperature: $F_{1, 116} = 22.905$, $P < 0.001$; effect of life history: $F_{1, 116} = 29.778$, $P < 0.001$). Females reared under the cold regime had a mean whole-body lipid content of 9.8%, which was 1.1% (95% C.I. = 0.8 – 1.5%) greater than in females reared under the warm regime (Figure 4.8). Maturing females had a mean whole-body lipid content of 9.9%, which was 1.3% (95% C.I. = 1.0 – 1.6%) greater than in smolting females (Figure 4.8).

For males, mean whole-body lipid content was 9.1% (± 0.28 SE). Males reared at cold temperatures had a mean whole-body lipid content that was 1.4% (95% C.I. = 0.9 – 1.9%) higher than males reared under warm temperature (ANOVA, $F_{1, 116} = 11.688$, $P < 0.001$). We did not detect differences in whole-body lipid content between life-history types in males (ANOVA, $F_{1, 116} = 0.815$, $P = 0.369$). However, the analysis of life-history types in males is likely confounded by the timing of our sampling relative to the individual developmental stage. Male samples included fully mature fish that were exuding milt. Fully mature males had a mean whole body lipid content of 8.0%, which was 1.3% (95% C.I. = 0.2 – 2.4%) lower than that of males in the process of maturation for reproduction in the subsequent spring. The lower whole-body lipid levels in fully mature males was likely due to energy loss during conversion of lipid from storage to gonad development, as well as loss of material during sampling.

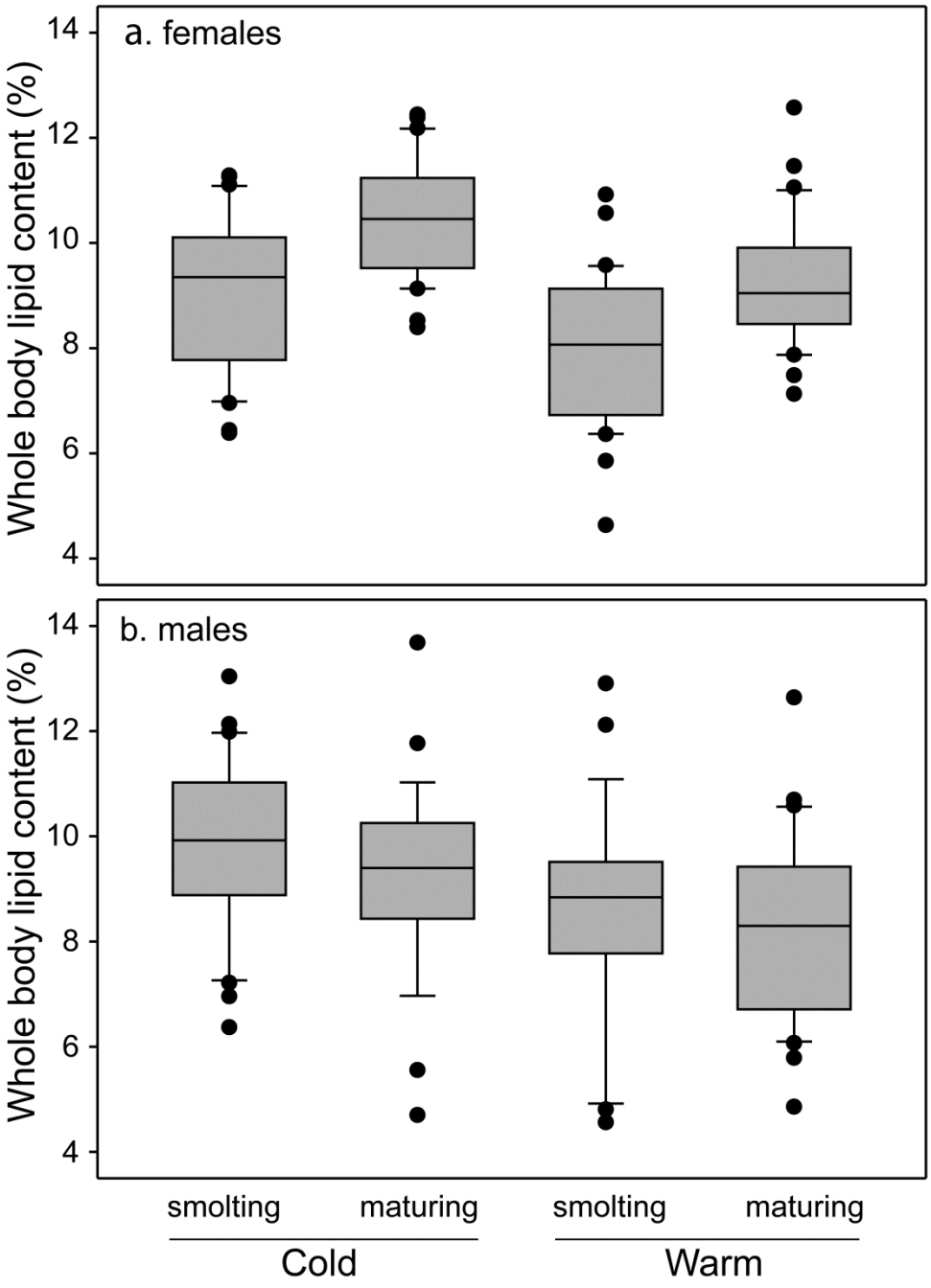

Figure 4.8. Whole-body lipid content for smolting and maturing (a) female and (b) male *O. mykiss* reared under a cold and warm thermal regime. Whiskers represent lines to data that are no more than 1.5 times the inter-quartile range. Top lines of boxes denote the 75th percentile, bottom lines the 25th percentile and middle lines the means. Filled circles denote outliers.

Discussion

In partially migratory salmonines, the decision to either mature as a freshwater resident or become anadromous is a phenotypically plastic response to the environmental opportunity for growth and development (Jonsson and Jonsson 1993; Hendry et al. 2004). By rearing a cohort of steelhead offspring under alternative thermal regimes, we determined how changes in temperature influenced the proportion of individuals surpassing conditional thresholds for the expression of alternative life histories. We found that the probability of adopting either freshwater-maturing or anadromous phenotypes in individual *O. mykiss* was influenced by patterns of individual growth, rearing temperature, and, in females, dominance status. Both male and female *O. mykiss* with the highest juvenile growth performance within their respective cohorts were more likely to initiate maturation, a result that is consistent with previous research on partially migratory salmonines (reviewed in Jonsson and Jonsson 1993; Dodson et al. 2013). For example, especially for males, a large body of literature demonstrates that faster growth and improved condition (i.e., higher lipid stores) during juvenile rearing leads to an increased probability of freshwater maturation (e.g., Saunders et al. 1982; Simpson 1992; McMillan et al. 2012). Fewer examples are available for females, but they generally follow a similar pattern whereby increased individual growth and condition promotes increased rates of residency (Wyusjak et al. 2009) and maturation (O'Connel and Gibson 1989; Morita and Nagasawa 2010). Thus, for a given set of environmental conditions, individuals having the highest growth performance are more likely to exceed the conditional thresholds triggering maturation.

When compared across thermal regimes, however, higher growth rates did not translate into increased rates of freshwater maturation. In fact, we observed the opposite trend. The

proportion of fish maturing under the warm thermal regime was 18 to 26% lower for females and males, respectively, despite an approximately 30 to 40% increase in final fish mass. A similar observation was made by Baum et al. (2005), who found that exposure to increased water temperatures elevated the length threshold for male parr maturity in Atlantic salmon (*Salmo salar*). If maturation decisions were based on somatic growth alone, we would expect that improved juvenile growth resulting from favorable increases in temperature would result in earlier maturation (Berrigan and Charnov 1994). Why did fewer fish mature under the warm thermal regime despite experiencing higher growth?

From a proximate standpoint, increased water temperature increases the metabolic maintenance costs for ectotherms, and as a consequence, less surplus energy may be available for storage and maturation. Energy reserves in the form of whole-body lipids are important precursors to the maturation process (Simpson 1992; Tocher 2003; Trombley and Schmitz 2013). A reduction in energy storage in a warmer environment, therefore, could reduce the probability of maturation. Our data on male whole-body lipid content are inconclusive, probably due to a mistiming of sampling with developmental stage in males. The high proportion of fully mature males in the sample of fish measured for whole-body lipid content probably confounded our analysis because of energy loss during conversion of lipid stores to gonads, and through loss of material during sampling. Consequently, we may have missed important conditional differences earlier in life that influenced male life-history expression.

Patterns of female maturation were consistent with this proximate view of the effects of temperature on life-history expression, however. Maturing females had higher mean whole-body lipid content than female smolts, and females reared under the cold thermal regime had higher

mean whole-body lipid content than those in the warm thermal regime. Previous studies of salmonids have also found a reduction in lipid storage with increasing water temperatures (Kepshire et al. 1983; Simpkins et al. 2003; McMillan et al. 2012). There appears to be a tradeoff between somatic growth and energy storage across different thermal environments (Tocher 2003; McMillan et al. 2012). For example, McMillan et al. (2012) found evidence for different energy allocation strategies in partially migratory *O. mykiss* populations inhabiting cool and warm tributaries of the John Day River, OR, USA. Juvenile *O. mykiss* had a larger size at age in warm streams but higher levels of whole-body lipid content in cold streams. McMillan et al. (2012) found that both individual fish size and whole-body lipid content were significant predictors of freshwater maturation in male *O. mykiss*, and a reduction in whole-body lipid level increased the estimated size threshold for maturation. Our results support the conclusions of McMillan et al. (2012) that warmer temperature regimes that maximize growth at the expense of lipids will reduce the probability of freshwater maturation. While the difference in whole-body lipid content among females in our study was small, differences are still likely to be biologically relevant, as McMillan et al. (2012) found that the probability of parr maturation in male *O. mykiss* increased by 33% for every 0.5% increase in whole-body lipid content. Thus, relatively small changes in levels of energy storage induced by the environment may be associated with large differences in rates of residency.

In addition to effects of individual growth and temperature, we found that dominance status influenced life-history expression in females. Females that were behaviorally dominant in competition for stream rearing space had lower rates of maturation, on average, compared with subordinate fish that emigrated from experimental streams. Similar to previous studies (e.g.,

Metcalfe et al. 1995; Cutts et al. 2001; McCarthy 2000), we found that dominant fish had higher SMR than subordinates. Females with higher dominance status also had slightly lower mean growth rates than subordinates, although growth differences were not statistically significant. Taken together, however, these results suggest that dominant females had proportionally less energy available for growth and maturation due to higher metabolic costs of maintenance. Forseth et al. (1995) found similar patterns in partially migratory brown trout (*Salmo trutta*) populations in which migratory phenotypes had higher metabolic demands than residents. Likewise, Morineville and Rasmusen (2003) found that anadromous brook trout (*Salvelinus fontinalis*) had higher metabolic energy costs during juvenile rearing than did residents. We did not observe an association between male dominance and the probability of maturation. This may be due to the lower costs of maturation in males relative to females. Male gonads may constitute as little as 3% of total somatic energy, whereas females may contain 30% of their total energy in gonads (Jonsson and Jonsson 2003; Jonsson et al. 2013). Because males need less energy for gonadal development, they may be less likely to be energetically constrained from maturation relative to females by intrinsic differences in metabolic costs.

Overall, our results demonstrate a strong influence of the environment on rates of anadromy and freshwater maturation in *O. mykiss*, but also highlight some of the challenges to predicting the effect of environmental change on life-history expression in phenotypically plastic species. While we found positive correlations between growth in body mass and rates of maturity within the same thermal environment, our results indicate that a change in somatic growth is not a robust predictor of life histories for populations exposed to different thermal regimes. Studies of non-salmonid fish have also demonstrated that temperature exerts an effect on maturation

independent of the effect of temperature on growth (Dhillon and Fox 2004; Kuparinen et al. 2011). In Japanese medaka (*Oryzias latipes*), age and size at maturity increased with increasing rearing temperature even when somatic growth rates were manipulated to remain constant across thermal regimes (Dhillon and Fox 2004). In a recent study, Kuparinen et al. (2011) demonstrated that increased rearing temperature induced a reduction in age and size at maturation in male nine-spined sticklebacks (*Pungitius pungitius*) that could not be explained solely by somatic growth differences across temperature treatments. These results, as well as our study, indicate that different thermal environments alter the correlations between size-at-age and the probability of maturation. The most likely explanation for this pattern is that somatic growth may be correlated with organism development, but it is not necessarily the cause of maturation. Growth and developmental rates are differentially sensitive to temperature in salmonines, as is common in other ectotherms (e.g., Bernardo and Reagan-Wallin 2002). Somatic growth represents one of several competing pathways by which energy is allocated within ectotherms (e.g., Forseth et al. 1999; Morineville and Rasmussen 2003), and by itself only partially reflects energy acquisition and allocation. For both males and females within our study, whole-body lipid content was significantly higher under cool temperatures. Thus, the “independent” effects of temperature on age and size at maturation observed elsewhere (Dhillon and Fox 2004; Kuparinen et al. 2011) may be explained by examining other components of energy allocation such as energy storage (e.g., McMillan et al. 2012).

Current efforts to model the effects of climate warming on life-history expression in salmonids focus on the bioenergetic effects of increased temperature on body size (e.g., Benjamin et al. 2013). Generally, model predictions suggest that an increase in freshwater-

maturing phenotypes will accompany increases in somatic growth due to favorable increases in stream temperature (Benjamin et al. 2013). Our study is one of the few to experimentally manipulate rearing temperature to determine the effects of different thermal regimes on life-history expression in partially migratory salmonids. The fact that our empirical results are at odds with model projections emphasizes the challenge of predicting the effects of climate change on species with complex life histories. Because temperature may alter energy allocation in important ways that are not captured by measuring somatic growth alone, a mechanistic understanding of the physiological responses to altered thermal regimes is needed to forecast effects of climate change.

Acknowledgements

We thank staff at ODFW's Clackamas River Hatchery for help obtaining fish for this experiment. Brian Nielsen and India Sloat helped with the construction of the experimental streams. Jerri Bartholomew, Don Stevens, and Jill Pridgeon provided access to the OSU's Salmon Disease Lab. Special thanks to Don Stevens for his assistance with fish rearing and experimental setup. Amy Lindsley, Haley Ohms, Matt Stinson, and Stephanie Saunders helped with data collection and processing. Funding for this work was provided by the USDA Pacific Northwest Research Station and the Oregon American Fisheries Society Carl Bond Memorial Scholarship. The use of animals in this experiment was conducted under OSU Animal Care and Use Permits # 3923 and 4019.

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Chapter 5—Conclusion

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Contemporary management and conservation of aquatic species increasingly incorporates perspectives from multiple subdisciplines within the fields of ecology and evolution. This is especially true of species with complex life histories, like *O. mykiss*. In the preceding chapters, I describe a series of experiments that attempt to understand linkages between individual variation in physiology and behavior, effects of this variation on energy acquisition and allocation, and resulting patterns of life-history expression. In Chapter 2, I establish a density-dependent link between intraspecific variation in physiology, behavior, and viability during early the initial stages of stream life in *O. mykiss*. Individuals with higher rates of energy metabolism were favored in competition for limited food and space in laboratory stream channels supplied with a consistent and abundant supply of food. As one in a suite of bioenergetic factors influencing life-history traits during subsequent life stages, selection on SMR during early ontogeny may influence subsequent life-history trajectories in phenotypically plastic species. In Chapter 3, I determined that variation in the spatial predictability of food resources can dramatically alter patterns of selection on energy metabolism in juvenile *O. mykiss* during the transition from dependence on maternal provisioning to independent stream life. Results from Chapters 2 and 3 establish that variation in ecological conditions during early life stages imposes different selection regimes on juvenile *O. mykiss* and results in physiologically divergent populations. Subsequent rearing experiments (Chapter 4) determined that behavioral dominance influences rates of anadromy and freshwater maturation, most likely through the association between SMR and territory acquisition. In addition to the effects of behavioral dominance, I observed a significant influence of sex, rearing temperature, and individual growth trajectories on the expression of anadromy and freshwater maturation. Partially migratory populations of *O. mykiss* maintain an exceptionally diverse portfolio of life-history strategies. Results from this

dissertation lend insight into a suite of physiological and behavioral processes influencing individual life histories.

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